Zoological Journal of the Linnean Society (1999), *125:* 239–278. With 9 figures
Article ID: zjls 1997.0163, available online at http://www.idealibrary.com on IDEAL

Evolutionary implications of hemipenial morphology in the terrestrial Australian elapid snakes

J. SCOTT KEOGH*

School of Biological Sciences A08, University of Sydney, Sydney NSW 2006, Australia

Received February 1997; accepted for publication September 1997

Venomous proteroglyphous or 'elapid' snakes are distributed across much of the tropical and subtropical world but are most diverse in Australia. Due to differing opinions of character weight and problems associated with high levels of homoplasy in traditionally used snake character systems, there is no well accepted hypothesis of phylogenetic relationships for the Australian elapids. Moreover, few or no synapomorphies have been identified to define many of the 20 currently recognized genera. As part of a re-evaluation of previous work, I have undertaken a survey of hemipenial morphology in this diverse radiation in a search for supraspecific synapomorphies. Up to 14 aspects of hemipenial morphology were scored on 756 museum specimens and provide the basis for hemipenial descriptions of 64 species of Australian elapid. Morphology is highly conservative at generic levels and supportive of a number of previously suggested phyletic groups, but divergent between putative monophyletic lineages. Hemipenial morphology provides synapomorphies that define seven, and possibly eight, monophyletic groups at subgeneric, generic, and suprageneric levels: (1) *Demansia*, *Oxyuranus*, *Pseudonaja*, and *Pseudechis* each display unique hemipenial morphologies but share a number of character states. The following groups each share unique hemipenial types: (2) *Simoselaps calonotus* and the *Simoselaps semifasciatus* species group, (3) *Vermicella* and the *Simoselaps bertholdi* species group, (4) *Cacophis* and *Furina*, (5) *Austrelaps*, *Echiopsis*, *Hoplocephalus*, *Notechis*, and *Tropidechis*, (6) *Drysdalia* and *Hemiaspis*, (7) *Rhinoplocephalus* and *Suta*, and (8) *Acanthophis* and *Denisonia*. Higher level associations also are identified. The organs of *Cacophis–Furina* and *Vermicella–Simoselaps bertholdi* clades are very similar in shape and differ in only a single character. The *Drysdalia–Hemiaspis* and *Rhinoplocephalus–Suta* clades share a hemipenial shape and also differ in only a single character. Where sample sizes were sufficient for comparison, hemipenes displayed little or no intraspecific variation.

ADDITIONAL KEY WORDS:—reptile – copulatory organ – systematics – evolution – Australia.

CONTENTS

Introduction 240
Monophyly of Australian elapids 241
Previous phylogenetic studies of Australian elapids 242

* Present address: Division of Botany and Zoology, Australian National University, Canberra ACT 0200, Australia. Email: scott.keogh@anu.edu.au

0024–4082/99/020239+40 $30.00/0

Male copulatory organs and squamate reptile systematics 243
Material and methods 244
Terminology 245
Results 251
Discussion 261
Higher level relationships 271
Acknowledgements 271
References 272
Appendix 277

INTRODUCTION

Adaptive radiations that are ancient and species-rich, and yet morphologically homogeneous, present special difficulties for inferring phylogenetic relationships at both low and high taxonomic levels. The problem is that such radiations often display high levels of homoplasy in morphological characters. For instance, retention of a morphologically conservative body plan (as in lineages such as teleost fish, birds, frogs, and snakes) may impose developmental constraints that reduce or limit opportunities for the evolution of new synapomorphies. More importantly in a systematic sense, innovations may arise numerous times in distantly related lineages due to these constraints. Because of this problem, taxonomic groupings within such radiations often are comprised of unnatural (paraphyletic) assemblages.

One group for which this problem arises is the cosmopolitan 'advanced snakes' or colubroids (Caenophidia), a diverse assemblage comprising over half of the world's 2750+ snakes species. Caenophidia comprises four major groups: the front fanged and venomous Viperidae (vipers, rattlesnakes), Atractaspidae, and Elapidae (coral snakes, cobras, sea snakes and their relatives), each defined by unique venom delivery systems, and the primarily non-venomous colubrids. Inferring evolutionary relationships within major lineages of colubroids has proven very difficult due to the extent of parallelisms in traditional morphological characters, characters that are then subject to often highly subjective (and varying) interpretations of their systematic weight by different authorities (Bellairs & Underwood, 1951; Dowling, 1967; Underwood, 1967a; Cadle, 1988, 1994). Hence, phylogenetic hypotheses, especially in regard to evolution of the venom delivery systems, have proven to be controversial (Cadle, 1982; Knight & Mindell, 1994; Zaher, 1994). One way to combat this problem is to search for and use character systems that may not be under direct form-induced constraints and thus are possibly less afflicted by high levels of homoplasy. Hemipenial morphology in squamate reptiles is such a character system (Vellard, 1928a, b, 1946; Dowling, 1967; Arnold, 1986a, b; Böhme, 1988). Indeed, morphological attributes of copulatory organs, especially the male intromittent organs, provide significant systematic characters in many groups of animals (Eberhard, 1985; Arnold, 1986a, b).

I have studied hemipenial morphology in the terrestrial Australian elapid snakes in an effort to identify natural groupings. I then compare this evidence with hypotheses of relationship presented by other authors and outline both corroborating and contradictory evidence. I propose no new classification schemes in this paper, nor do I attempt to redefine any higher level groupings. I defer providing detailed group definitions until completion of a full cladistic analysis with other morphological character systems. I will first briefly introduce elapid snakes, and terrestrial Australian

elapids in particular, and then review male copulatory organ morphology as it pertains to snake evolution.

Monophyly of Australian elapids

Elapids (variously referred to families Elapidae and Hydrophiidae [Smith, Smith & Sawin, 1977] or family Elapidae [Underwood, 1967a; Dowling, 1974]) number approximately 300 species in 61 genera and are distributed across much of the tropical and subtropical world including the Americas, Africa, Asia, Melanesia, Australia, and the oceans (Mengden, 1983; Golay *et al.*, 1993). Elapids are primarily defined by their unique proteroglyphous venom delivery system comprised of two small erect canaliculate fangs at the end of the maxilla (McDowell, 1968; McCarthy, 1985). Elapids are represented by a number of distinct lineages including the American and Asian coral snakes, the African and Asian cobras, African mambas, Asian kraits, the partially terrestrial sea kraits, the fully aquatic true sea snakes, and the Australian and Melanesian terrestrial elapid groups. The familial status of other more obscure groups such as the African *Atractaspis* and *Homoroselaps* remain controversial but they may be basal members of the elapid radiation (McCarthy, 1985; McDowell, 1986; Underwood & Kochva, 1993).

Of the various elapid groups, the terrestrial Australian radiation is the most diverse at both generic and specific levels with 20 currently recognized genera and approximately 88 species (for the purposes of standardization, I use the recent and well-accepted classification of Hutchinson [1990] throughout this paper except where explicitly stated otherwise). At least two other elapid groups are closely associated with the terrestrial Australian radiation. McDowell (1970) divided elapid snakes into two subgroups based on mobility of the palatine bone and the morphological attributes associated with its kinesis: the 'palatine draggers' and 'palatine erectors'. Palatine draggers include all terrestrial Australo-Papuan elapids (except the Bougainville Island *Parapistocalamus*) and the diverse true sea snakes, while palatine erectors include terrestrial African, Asian and American elapids, *Parapistocalamus*, and the partially marine *Laticauda*. Except for the placement of *Laticauda*, recent phylogenetic analyses largely have supported this division, particularly the close association of true sea snakes and terrestrial Australo-Papuan elapids (McDowell, 1967, 1969a,b, 1970, 1972; Mao *et al.*, 1977, 1978, 1983; Minton, 1981; Minton & da Costa, 1975; Voris, 1977; Cadle & Gorman, 1981; Coulter, Harris & Sutherland, 1981; Schwaner *et al.*, 1985; Tamiya, 1985; Rasmussen, 1994; Slowinski, Knight & Rooney, 1997; Keogh, 1998; Keogh, Shine & Donnellan, 1998). Although the relationship of *Laticauda* to other elapid groups has been contentious, there is now much evidence to suggest that *Laticauda* is associated with the Australo-Papuan 'palatine dragger' radiation rather than the 'palatine erectors' (Cadle & Gorman, 1981; Mao *et al.*, 1983; Slowinski *et al.*, 1997; Keogh, 1998; Keogh *et al.*, 1998). The endemic terrestrial Melanesian and Pacific island elapid genera *Toxicocalamus* and *Aspidomorphus* (with nine and three species respectively) and the monotypic *Loveridgelaps*, *Micropechis*, *Salomonelaps* and the Fijian *Ogmodon* also are part of McDowell's 'palatine dragger' radiation (McDowell, 1967, 1969a, 1970, 1986) with at least some of these genera part of the 'Australian' elapid ingroup while others are basal to it (McDowell, 1967, 1969a, 1970; Schwaner *et al.*, 1985; Keogh, 1998; Keogh *et al.*, 1998).

While acknowledging uncertainties as to the exact composition of the 'Australian' elapid group, its limits, and the other lineages with which it is affiliated, the terrestrial Australian elapids form a convenient unit and are the subset of elapids to which I restrict myself in this paper. Terrestrial Australian elapids are also a convenient biogeographic unit because they are highly endemic. Only six of the approximately 88 species also are found outside the continent (*Acanthophis antarcticus*, *Demansia papuensis*, *Furina tristis*, *Oxyuranus scutellatus*, *Pseudechis australis*, and *Pseudonaja textilis*) and of these, only the death adder *A. antarcticus* extends beyond New Guinea westward to the Indonesian island of Ceram (Cogger & Heatwole, 1981). Hemipenial morphology of other related elapid groups and the evolutionary implications of this morphology will be described elsewhere.

Previous phylogenetic studies of Australian elapids

Of the various elapid lineages, the terrestrial Australian elapids are the most morphologically diverse, although they tend to be conservative in traditional character systems used in snake systematics. Early workers (i.e. Krefft, 1869; Loveridge, 1934; Kinghorn, 1956) disagreed on many taxonomic issues, particularly in regard to generic level boundaries, and their taxonomic decisions were based on re-interpretations of the same small and incomplete data sets on external morphology and osteology first outlined by Günther (1858) and Boulenger (1896) (Mengden, 1983; Cogger, 1985). Thus, Australian elapids have had a complicated taxonomic history dominated by instability and strongly differing opinions (reviewed by Mengden, 1983 and Keogh, 1997). This is exemplified by the fact that only one of the 20 currently recognized genera has not been taxonomically altered in the past 30 years (Mengden, 1983; Hutchinson, 1990). Much of this taxonomic instability can be attributed to the relatively few characters used to define groups, their conservative nature in traditional taxonomic characters, and differing weights given to characters by different authorities (Mengden, 1983; Cogger, 1985; Hutchinson, 1990; Shea *et al.*, 1993). As noted by Cogger (1985) the taxonomic history seems to reflect a preoccupation with names and not with the biology of the animals. Some subgroups are hypothesized to be monophyletic but this contention is supported by few, or in some cases, no synapomorphies. This deficiency has stimulated several systematic studies utilizing both morphological and molecular approaches.

The work of Worrell (1955, 1956, 1960, 1961, 1963a–c) on the cranial osteology and dentition of Australian elapids was the first major move away from the traditional small data sets used by previous authors. Worrell's work resulted in considerable taxonomic changes, primarily the splitting of the then very large genus *Denisonia* into seven genera. This study was followed by the work of McDowell (1967, 1969a, b, 1970), who examined relationships of Australo-Papuan terrestrial elapids using various aspects of cranial osteology, dentition, venom gland musculature, and hemipenial morphology. McDowell was the first to move away from alpha level taxonomy by inferring relationships among species and genera. Wallach (1985) quantified primarily morphological characters in the first cladistically analysed data set used to infer relationship among Australian elapids, using *Naja melanoleuca* as the outgroup. Approximately half of Wallach's (1985) 50 characters were drawn from internal soft anatomy, primarily lung morphology, while the remaining characters were various aspects of external morphology, ecology, and other miscellaneous

characters obtained from the literature. Mengden (1982, 1985a, b) studied gross chromosome structure and number in virtually all Australian elapid species, and identified 10 karyomorph groups based on both karyotypes and shared fixed differences in chromosome banding patterns. The cytogenetic data, combined with an electrophoretic analysis of 30 enzyme systems, resulted in Mengden's (1985a, b, hypothesis of relationships for Australian elapids. Schwaner *et al.* (1985) used immunological distance methods to estimate phylogenetic relationships among terrestrial Australian elapids and sea snakes and also included some Asian and African species. In addition to supporting the monophyly of terrestrial Australian elapids and true sea snakes to the exclusion of Asian and African elapids, these workers also were able to identify a number of subgroups within the terrestrial Australian lineage.

Despite a relatively broad level of agreement in basic phylogenetic structure among these various studies, few higher nodes are unambiguously supported by synapomorphic characters, and the studies are contradictory at various levels and for various clades. However, the monophyly of most genera appears to be fairly stable. Hutchinson (1990) critically examined and interpreted the recent phylogenetic work and was able to distil the information presented by the various authors and provide a generic level classification for the terrestrial Australian elapids. Hutchinson's classification scheme has subsequently been adopted by Cogger (1992) and it is this summation of previous phylogenetic work that I use as the taxonomic framework for my own re-evaluation of the phylogenetic work of previous authors.

Male copulatory organs and squamate reptile systematics

The male copulatory organs or hemipenes of squamate reptiles are paired, blind, tubular structures that lie in the base of the tail when in their retracted state and protrude from the lateral edges of the vent when in their everted (functioning) state (Cope, 1900; McCann, 1946; Dowling & Savage, 1960). The outer surface of the everted organ displays a deep sperm-transporting thick-lipped groove called the sulcus spermaticus that bifurcates near the free distal end in many snake groups, and generally displays one or more types of ornamentation (Dowling & Savage, 1960). When in the retracted state, the functionally outer surface (and thus the ornamentation and sulcus spermaticus) is on the *inner* surface of the blind tube, that is the hemipenis is carried 'inside-out' in the tail base when not in use (Cope, 1894).

Snake hemipeneal morphology is quite diverse, with phylogenetically useful differences in size, shape and ornamentation (Dowling & Savage, 1960). Cope (1893, 1894, 1895, 1900) was the first to apply this new character system to snake systematics, studying over 200 species from most major snake lineages, in an attempt to produce a classification that more accurately reflected their evolutionary history. Since his time, many other workers have shown that hemipenial morphology is especially useful for inferring evolutionary relationship and defining monophyletic groups in snakes (i.e. Dunn, 1928; Vellard 1928a, b, 1946; Bogert, 1940; Domergue, 1962; Dowling, 1959; Dowling & Savage, 1960; Robb, 1960, 1966a,b; Clark, 1964; Dowling, 1967; Myers & Trueb, 1967; Branch & Wade, 1976; Branch, 1981, 1986; Jenner & Dowling, 1985; Keogh, 1996; Cadle, 1996) as well as lizards (i.e. Cope, 1896; Rosenberg, 1967; Arnold, 1973, 1983, 1986a; Böhme, 1971, 1988; Presch, 1978; Branch, 1982; Klaver & Böhme, 1986; Card & Kluge, 1995).

Part of the popularity of using hemipenial morphology in squamate systematics can be attributed to its usefulness at various taxonomic levels. While their utility for inferring relationship at higher taxonomic levels may be limited, hemipenes are excellent indicators of relationship at specific and generic levels (Bogert, 1940; Arnold, 1986b; Branch, 1986; Böhme, 1988). There tends to be relatively little intraspecific variation and some groups show strong morphological conservatism within genera, while others display significant interspecific differences (Vellard, 1928a, b, 1946; Dowling & Savage, 1960; Dowling, 1967). While hemipenial morphology in some lizards can show seasonal variation in size and ornamentation (Böhme, 1971; Arnold, 1986b; Branch, 1982), this is not a problem in snakes (Volsøe, 1944; Branch, 1982; and this study). Further, a number of authors have stated or implied that because hemipenial morphology in squamate reptiles has no obvious correlation with ecology, diet, locomotion, and so on, it may be less subject to homoplasy and thus may provide greater insight into phylogenetic relationships (Dowling, 1967; Böhme, 1971, 1988; Arnold, 1986b; Branch, 1986; Klaver & Böhme, 1986).

Various workers have provided hemipenial descriptions of elapid species (i.e. Cope, 1893, 1894; McCann, 1946; Bogert, 1940; Dowling & Duellman, 1978; Mao *et al.*, 1984) or used hemipenial morphology to infer relationship among elapid groups (i.e. McDowell, 1967–1987; Savitzky, 1979; Slowinski, 1994, 1995). Hemipenial morphology of Australo-Papuan elapids and sea snakes has been studied by McDowell (1967–1987) who used it in his studies of evolutionary relationships. However, McDowell's studies were based on dissected organs rather than everted organs. While his descriptions are accurate and detailed, it is now known that dissected organs can show little resemblance to fully everted organs, particularly in length, shape and orientation (McCann, 1946; Dowling & Savage, 1960; Dowling, 1967; Branch, 1986, Böhme, 1988). In this paper I describe the results of an extensive survey of hemipenial morphology in most species and in each clade of terrestrial Australian elapid snake, based on everted organs.

MATERIAL AND METHODS

I searched through each of the seven major Australian natural history collections for fully or partially everted hemipenes from terrestrial Australian elapid snakes (Australian Museum, South Australian Museum, Northern Territory Museum of Arts and Sciences, Queensland Museum, National Museum of Victoria, Western Australian Museum, and CSIRO Australian National Wildlife Collection—see Appendix). A total of 756 specimens with fully or partially everted hemipenes were examined and form the basis for hemipenial descriptions of 64 of the 88 currently recognized species of terrestrial Australian elapid snake. Sample sizes vary from one hemipenis (in four species) to 85 (in the *Notechis* complex), with a mean sample size of 8.8 per species. Small sample sizes are quite adequate for hemipenial descriptions because intraspecific variation is generally small or non-existent and the variation that may be present often only reflects artifacts of preservation (Arnold, 1986a, b; Böhme, 1988; and this study).

The majority of hemipenes were examined while still attached to the snake, although the South Australian Museum maintains a collection of hemipenes that

have been carefully everted, tied off, detached from the snake, and housed separately. Each hemipenis was examined and scored for each of the characteristics listed below. However, as noted by Branch (1986), many everted hemipenes housed in museum collections are only partially everted, badly preserved, or damaged, thus their taxonomic value is limited. When this was the case, only unaffected characteristics were scored (e.g. presence or absence of basal hooks, basal nudity). When only partially everted or badly preserved hemipenes were available for a species, this species was not included in the study. All descriptions are based on fully everted hemipenes.

In many cases, different species (or genera) display virtually identical hemipenial morphologies. For these cases, only a single full description is given with the small interspecific differences noted. For the purposes of illustration, representative voucher specimens were chosen from each genus and hemipenial type. Subtle differences that may occur in other species are described in the text. All drawings were made with the aid of a camera lucida.

Terminology

I have tried to follow closely the terminology outlined by Dowling and Savage (1960) and the further modifications outlined by McDowell (1961, 1968), Myers and Trueb (1967), and Branch (1986). However, I have slightly altered some character definitions or have added or subdivided characters that would not fit easily into these schemes to better reflect diversity in the hemipenial morphology of the Australian elapids and facilitate the tabulation of a large number of specimens. Each of the characters recorded are briefly defined below and I have noted where my definitions differ from those of the above authors (see Fig. 1). Symbols used in Table 1 are shown in parentheses.

Gross morphology

I follow Myers and Trueb (1967) and use the terms *sulcal* to refer to the side of the hemipenis on which the sulcus spermaticus runs (medial of Dowling & Savage, 1960) and *asulcal* to refer to the side opposite the sulcal surface (lateral of Dowling & Savage, 1960). I use the term *lateral* to refer to the surfaces between the sulcal and asulcal surfaces and the terms *proximal* and *distal* to refer to the basal and free apical portions respectively of the *everted* organ.

Shape. Hemipenial shape is difficult to define unambiguously because some hemipenes are intermediate between the three traditionally used character states (single, bilobed, divided) as defined by Dowling & Savage (1960). The nature of hemipenial shape is often more complex than these categories can describe, which led Branch (1986) to recognize intermediates. I have adopted these intermediates with slight modifications. Total hemipenial length (measured from base to top of the longest apical lobe if asymmetrical) and distance from base to crotch (division of apical lobes if present) was measured with digital callipers, on fully everted hemipenes only. Base to crotch length was then expressed as a proportion of total length to give an indication of the degree of apical differentiation and the following categories were recognized: 100–90% is *simple* (S), 89–75% is *shallowly-forked* (SF), 74–50% is *forked* (F), and 49–25% is *deeply forked* (DF), (Branch's [1986] *simple* and *shallowly-forked*

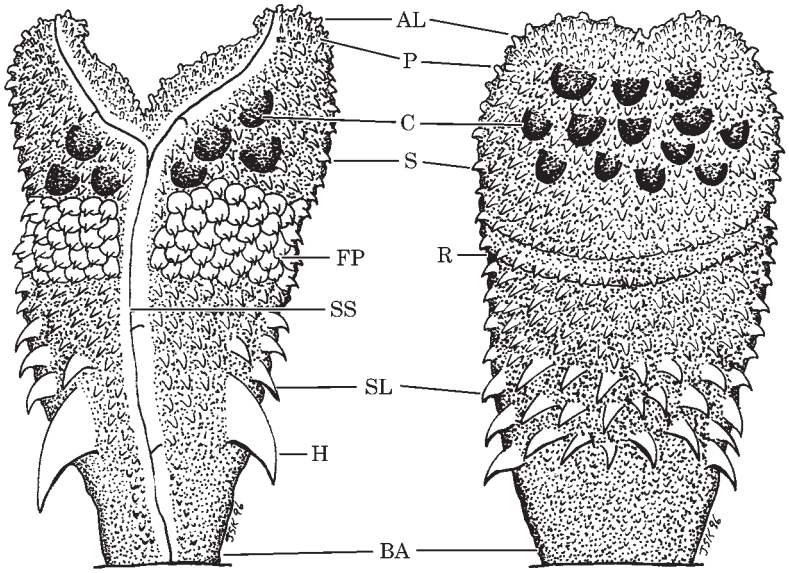

Figure 1. Composite sulcal (left) and asulcal (right) hemipenes to illustrate the relevant morphological features found among Australian terrestrial elapid snakes. AL = apical lobes, P = papillae, C = calyces, S = spines, FP = fleshy protuberances, R = ridges, SS = sulcus spermaticus, SL = spine line, H = basal hooks, BA = base.

categories were 100% and 99–75%, respectively. His last category of 24–1% was not applicable to the Australian elapids studied). Further differentiation of the apical lobes may be present in some species and this was scored separately (see 'apical differentiation' below).

Sulcus spermaticus. The sperm transporting canal lies on the surface of the everted hemipenis and runs longitudinally toward the apical lobes. It may be either simple and undivided or bifurcate into two separate canals towards or on the apical lobes (Dowling & Savage, 1960). The nature of sulcus division is now known to display a wide range of conditions. Various authors have described sulcus orientation but the terminology used has not been consistent. Branch (1986) standardized terminology for sulcus condition and recognized eight types. I found it difficult to classify sulcal condition clearly among the Australian elapids because they appeared intermediate between two types based on my interpretation of Branch's definitions. All Australian elapids examined possess a sulcus that bifurcates in or just below the crotch, and the forks continue up the apical lobes facing the mid-line of the organ, the *centripetal sulcus* of Branch (1986) (the ortho-centripetal sulcus of McDowell, 1968). However, while much of the sulcal fork faces the mid-line, the termination points of the sulcal forks generally face *away* from the mid-line in the Australian elapids, the *centrifugal sulcus* of Branch (1986). Branch did not indicate where the termination of the forks occurred in the centripetal sulcus. Given the apparent ambiguity in definitions with regard to the Australian elapids, I consider them to have a centripetal sulcus but with forks terminating away from the mid-line. Other terms have been used for other elapid groups. Slowinski (1994) described Asiatic elapid *Bungarus* hemipenes as centrolineal after Myers and Campbell (1981)—the semi-centrifugal sulcus of

Branch (1986). However, only asulcal surfaces were figured and thus I was unable to determine whether the different scoring of sulcal condition is due to real morphological differences or simply different interpretations of sulcus definitions, or both.

Apical differentiation. Most Australian elapids display hemipenes that simply terminate in rounded or slightly pointed apical lobes of varying length and exhibit various types of ornamentation (see below), thus apical differentiation is *absent* (A). However, some groups display distinctive structures at the distal ends of the apical lobes. Apical lobes may be *disk* shaped (DISK) and terminate in a flat and nude disk that is separated from the surrounding hemipenis by raised lips, or display *terminal awns* (AWN) in which the distal portion of the apical lobes is separated from the proximal portion by a constriction from which long, thin projections extend.

Basal hooks. Several Australian elapids display very large spines on either side of the sulcus spermaticus near the base of the organ (termed basal hooks by Dowling & Savage, 1960). Basal hooks were scored as *present* (P) or *absent* (A) and further denoted as *weak* (wk) in some species where they are not as pronounced.

Spine line. Most Australian elapids display from one to several rows of larger spines that begin on either side of the sulcus spermaticus, continue around the asulcal surface, and lie near the base. These spines range from being only slightly larger (though generally more dense) to much larger than the spines that cover the rest of the hemipenis. Depending on the species, the spine line can be found anywhere from just distal to the base to the mid-section of the hemipenis. Spine line condition was scored as *present* (P) or *absent* (A). When the spine line is present it can show interspecific differences in expression. Therefore I further differentiate spine line condition by noting if it is *strong* (st), *weak* (wk), or *very weak* (vwk).

Medial projection. Some Australian elapids display a rounded medial projection that protrudes between the apical lobes (if the apical lobes are present) or between the forks of the sulcus spermaticus on top of the hemipenis (if the apical lobes are absent). This character was scored as either *present* (P) or *absent* (A). I further noted if the medial projection was *ornamented* (O) with small spines or papillae or *nude* (N).

Ornamentation

The hemipenes of snakes generally display ornamentation such as spines, calyces, papillae, flounces, some combination of these, or they may be completely nude. Each of these ornamentation types was scored separately following the definitions of Dowling & Savage (1960).

Ornamentation. If the ornamentation type is homogeneous and uniform over the entire surface of the hemipenis it is described as *undifferentiated* (UD) (e.g. spines only). A *differentiated* (D) hemipenis has at least two types of ornamentation (e.g. spines and calyces).

Base ornamentation. The basal portion of the hemipenis may be *ornamented* (O) with small spines or *nude* (N) with no obvious ornamentation.

Calyces. Dowling & Savage (1960) defined calyces as ". . . a complex ornamentation of retiform ridges." I define calyces somewhat differently because I recognize another character 'ridges' below. Calyces are small complex cup-shaped depressions that

TABLE 1. Summary of hemipenial morphology in the terrestrial Australian elapid snakes. Symbols as follows: S = simple, SF = shallowly forked, F = forked, DF = deeply-forked, A = absent, P = present, AWN = terminal awns, Disk = disk apical lobes, D = differentiated, UD = undifferentiated, O = ornamented, N = nude, VSm = very small, Sm = small, M = medium, L = large, vwk = very weak, wk = weak, st = strong, sp = spinulate, scal = scalloped, pap = papillate, caly = calyces, ridg = ridges. See Material and methods for full character descriptions and the Appendix for museum specimens examined.

Species	*n*	Shape	Apical Differentiation	Basal hooks	Spine line	Medial projection	Ornamentation	Base	Calyces	Ridges	Fleshy protuberances	Spine size	Papillae	Micro ornamentation
GROUP 1:														
Demansia atra	12	S	A	P	P	A	D	O	P	P	A	Sm	P	pap
Demansia olivacea	5	S	A	P	P	A	D	O	A	P	A	L	P	—
Demansia papuensis	7	S	A	P	P(st)	A	D	O	P	P	A	Sm	P	pap
Demansia psammophis	16	S	A	P	P	A	D	O	P	P	A	Sm-L	P	pap
Demansia torquata	5	S	A	P	P(st)	A	D	O	A	P	A	M/Sm	P	—
Pseudechis australis	28	SF	A	A	P	A	D	O	P	P	P	VSm	P	pap/sp
Pseudechis guttatus	13	SF	A	A	P(st)	A	D	O	A	P	P	VSm	P	pap/sp
Pseudechis porphyriacus	37	SF	A	A	P	A	D	O	P	P	P	VSm	P	pap
Pseudonaja affinis	11	SF	A	P	P	A	D	O	P	A	A	VSm	P/A	scal and/or sp
Pseudonaja guttata	8	SF	A	P(wk)	P	A	D	O	A	A	A	VSm	A	pap
Pseudonaja inframaculata	22	SF	A	P	P	A	D	O	P	P/A	A	VSm	P	scal/pap/or sp on ridg or caly
Pseudonaja ingrami	7	SF	A	P(wk)	P	A	D	O	P	P	A	VSm	P	scal/pap/sp on ridg or caly
Pseudonaja modesta	12	SF	A	P	P	A	D	O	P	P	A	VSm	P	scal and/or pap
Pseudonaja nuchalis	56	SF	A	P	P	A	D	O	P/A	P/A	A	VSm	P	scal/pap/or sp on ridg and caly
Pseudonaja textilis	77	SF	A	P	P	A	D	O	P	P/A	A	VSm	P	scal/pap/or sp on ridg and caly
Oxyuranus microlepidotus	4	SF	A	A	P	A	D	O	P	P	A	VSm	P	pap
Oxyuranus scutellatus	10	SF	A	A	P	A	D	O	P	P	A	VSm	P	pap
GROUP 2:														
Simoselaps approximans	2	SF	A	A	P(wk)	A	D	O	A	A	A	M	P	—
Simoselaps australis	9	SF	A	A	P	A	D	O	A	A	A	M	P	—
Simoselaps bimaculatus	2	?	?	A	P(wk)	?	D	O	A	A	A	M	?	—
Simoselaps calonotus	3	SF	A	A	P(wk)	P(wk)	D	O	A	A	A	M	P	—
Simoselaps fasciolatus	7	SF	A	A	P	A	D	O	A	A	A	M	P	—
Simoselaps incinctus	5	SF	A	A	P(wk)	A	D	N	A	A	A	M	P	—
Simoselaps semifasciatus	8	SF	A	A	P	A	D	O	A	A	A	M	P	—
GROUP 3:														
Simoselaps anomalus	2	F	A	A	A	A	D	O	A	A	A	M	P	—
Simoselaps bertholdi	13	F	A	A	A	A	UD	O	A	A	A	M	A	—
Vermicella annulata	6	F	A	A	A	A	UD	O	A	A	A	M	P	—
Vermicella intermedia	3	F	A	A	A	A	UD	O	A	A	A	M	P	—

TABLE 1. *continued*.

Species	*n*	Shape	Apical Differentiation	Basal hooks	Spine line	Medial projection	Ornamentation	Base	Calyces	Ridges	Fleshy protuberances	Spine size	Papillae	Micro ornamentation
GROUP 4:														
Cacophis squamulosus	5	F	AWN	A	P(vwk)	A	D	N	A	A	A	M	P	—
Furina diadema	2	F	AWN	A	P(vwk)	A	D	N	A	A	A	L	P	—
Furina dunmalli	3	F	AWN	A	P(vwk)	A	D	N	A	A	A	M	P	—
Furina ornata	5	F	AWN	A	P(vwk)	A	D	N	A	A	A	L	P	—
Furina tristis	2	F	AWN	A	P(vwk)	A	D	N	A	P	A	M	P	pap/sp
GROUP 5:														
Austrelaps complex	56	SF	A	A	P(wk)	A	D	O	P	A	A	Sm	P	pap/sp
Echiopsis curta	6	SF	A	A	P(st)	A	D	O	A	A	A	M	P	—
Hoplocephalus bungaroides	1	SF	A	A	P(st)	A	D	O	A	A	A	M	P	—
Hoplocephalus stephensi	1	SF	A	A	P(st)	A	D	O	A	A	A	M	P	—
Notechis complex	91	SF	A	A	P(st)	A	D	O	P(wk)	A	A	Sm	P	pap/sp
Tropidechis carinatus	4	SF	A	A	P(st)	A	D	O	A	A	A	Sm	P	—
GROUP 6:														
Drysdalia coronata	6	S	A	A	P	A	D	O	A	A	A	M	P	—
Drysdalia coronoides	10	S	A	A	P	A	D	O	P	A	A	M	P	pap/sp
Drysdalia mastersi	11	S	A	A	P	A	D	O	A	A	A	M	P	—
Drysdalia rhodogaster	1	S	A	A	P	A	D	O	P	A	A	M	P	pap/sp
Hemiaspis domeli	5	S	A	A	P	A	D	O	A	A	A	M	P	—
Hemiaspis signata	13	S	A	A	P(st)	A	D	O	P	A	A	M	P	pap/sp
GROUP 7:														
Rhinoplocephalus bicolor	4	S	A	A	P(st)	P(O)	D	N	A	A	A	M	P	—
Rhinoplocephalus boschmai	5	S	A	A	P	P(N)	D	N	A	A	A	M	P	—
Rhinoplocephalus nigrescens	22	S	A	A	P(st)	P(O)	D	N	A	A	A	M	P	—
Rhinoplocephalus nigrostriatus	2	S	A	A	P	P(O)	D	N	A	A	A	M	P	—
Suta fasciata	3	S	A	A	P(wk)	P(N/O)	D	N	A	A	A	M	P	—
Suta flagellum	10	S	A	A	P(wk)	P(O)	D	N	A	A	A	M	P	—
Suta gouldi	6	S	A	A	P(st)	P(N)	D	N	A	A	A	M	P	—
Suta monachus	4	S	A	A	P(st)	P(N)	D	N	A	A	A	M	A	—
Suta nigriceps	10	S	A	A	P(st)	P(O)	D	N	A	A	A	M	P	—
Suta ordensis	3	S	A	A	P(st)	P(O)	D	N	A	A	A	M	P	—
Suta punctata	4	S	A	A	P(wk)	P(O)	D	N	A	A	A	M	P	—
Suta spectabilis	19	S	A	A	P(wk)	P(N)	D	N	A	A	A	M	P	—
Suta suta	35	S	A	A	P(st)	P(N/O)	D	N	A	A	A	M	P/A	—
GROUP 8:														
Acanthophis antarcticus	15	DF	DISK	A	A	A	UD	O	A	A	A	M	A	—
Acanthophis praelongus	1	DF	DISK	A	A	A	UD	N	A	A	A	M	A	
Denisonia devisi	3	F	A	A	P(wk)	A	D	N	P	P	A	M	P	pap/sp

display raised lipped edges that themselves may display their own ornamentation (see micro-ornamentation below). Calyces generally run in lateral parallel rows around the organ and tend to be more numerous on the asulcal surface and around the apical lobes. Calyces were scored as *present* (P) or *absent* (A).

Ridges. Some Australian elapids display ridges that are ordered series of raised parallel rows of fleshy tissue that display their own ornamentation (see micro-ornamentation below). I differentiate between ridges (which are raised and fleshy) and parallel rows of spines (which are not raised or fleshy) which also occur in a number of species (see 'spine size' below). Ridges are generally found on the asulcal surface of the organ extending around the sides toward the sulcus and below the calyces if present. Most of the species that display ridges also possess calyces. The line of demarcation between these ornamentation types is often weak and they appear to grade into each other. In a few species, ridges are found between the apical lobes. This character was scored as *present* (P) or *absent* (A) and was not defined by Dowling & Savage (1960).

Fleshy protuberance. Some species of Australian elapids display distinctive fleshy protuberances on the hemipenial surface that form the swollen bases of spines. Each of these spine-bearing bumps abuts its neighbour, giving the hemipenis the unique appearance of being covered with a 'rough skin'. Fleshy protuberances occur instead of, or in addition to, calyces and/or ridges. This characteristic was scored as *present* (P) or *absent* (A) and was not defined by Dowling & Savage (1960).

Spine size. All species of Australian elapids examined display spines on the hemipenis. Spines generally are not distributed evenly over the organ but tend to increase in density toward the apical lobes and on the asulcal surface. Some species display sections of the hemipenis with spines arranged in linear rows (not equivalent to 'ridges'). Spines show interspecific differentiation in relative size, some species have quite small spines while others show intermediate or large spines. Spine size was scored only for the spines that cover most of the hemipenial surface, the spines of the spine line and basal hooks (above) were not included. After examining spine size variation in the Australian elapids I was able to score relative spine size as *small* (Sm), *medium* (M), or *large* (L). Spine size was not defined in Dowling & Savage (1960).

Papillae. Papillae are small fleshy projections that are rounded at the tip (not sharp and calcified like spines) and are found on and between the apical lobes in most but not all species of Australian elapids examined. This character was scored as *present* (P) or *absent* (A).

Micro-ornamentation. When calyces or ridges are present, they often display micro-ornamentation on their edges. Calyces or ridges may be *scalloped* (scal) with rounded contoured edges, *papillate* (pap) with small papillae, or *spinulate* (sp) with small spines.

Dowling & Savage (1960) recommended recording length of the hemipenis relative to the number of subcaudal scales and conceded that while length does show some variation, it is generally minimal. After examination of a large number of hemipenes, it became evident that length of everted organs is largely dependent on how well the hemipenis was everted and preserved at the time of fixation. Over filling of the organ with preservative can extend its natural length and under filling or failure to cut the retractor muscles can produce preserved hemipenes that are not fully everted

and thus provide inaccurate lengths. Because of the unavoidable inaccuracies, I do not report hemipenial length except for the representative hemipenes I have figured.

RESULTS

Hemipenial morphology of 64 of 88 species, and 19 of the 20 genera (the monotypic *Elapognathus minor* was not available) of terrestrial Australian elapids are here described. Intraspecific variation was virtually nonexistent and most of the intraspecific variation that was present can be attributed to preservation artifacts. Hemipenial morphology tended to be highly conservative at supraspecific levels; no single species had a truly unique hemipenis. Instead, hemipenial types were identified at subgeneric, generic, and suprageneric levels. I was able to easily divide Australian elapids into eight groups based primarily on overall similarity in hemipenial shape (Figs 2–7). Descriptions are provided at the appropriate level of differentiation. For example, in Group 1 each of the four included genera display unique hemipenes, so a description is given for each genus (all examined species within each genus displayed the same hemipenial type), while Group 3 is comprised of species from two genera, the species of which share a hemipenial type, thus a single description is given for all members. However, all characteristics were scored for each species and these data are summarized in Table 1. A representative of each hemipenial type or genus was figured and the reader should refer to the figures as well as the descriptions.

(1) *Demansia*, *Oxyuranus*, *Pseudechis* and *Pseudonaja*

Demansia. Hemipenes were examined from *D. atra*, *D. olivacea*, *D. papuensis*, *D. psammophis*, and *D. torquata. Demansia* are unique among terrestrial Australian elapids in the possession of single (nonlobate) and bulbous shaped hemipenes (Fig. 2A). The bulbous nature of the organ is evident from sulcal, lateral, and asulcal views as well as from the top of the organ. The hemipenes of most other Australian elapid species display some degree of apical differentiation. In *Demansia*, the sulcus spermaticus divides near the top of the organ in most individuals examined with the sulcal forks continuing to the top of the small apical lobes. The spine line is very distinct, comprised of large and heavily calcified spines, and is particularly strong in *D. papuensis* and *D. torquata.* The spine line begins with large and pronounced basal hooks, a feature shared only with *Pseudonaja* among the terrestrial Australian elapids. The sulcal surface is covered with an even distribution of spines that vary in size between species. The spines are quite small in *D. atra* and *D. papuensis*, slightly larger in *D. torquata*, and fairly large and less dense in *D. olivacea*. *Demansia psammophis* specimens display the full range of spine size from small and dense to large and sparse. *Demansia* also is unique in the arrangement of spines on the organ. Spines on sulcal, lateral, and asulcal surfaces are arranged in very regular parallel rows (Fig. 2A). These parallel rows are particularly pronounced in *D. atra* and *D. papuensis* and less pronounced in *D. olivacea* and *D. psammophis*. Papillate calyces are present in *D. atra*, *D. Papuensis*, and *D. psammophis* but are pronounced only on the asulcal surface. The apical tips of all species are covered with small papillae while the base is ornamented with small spines.

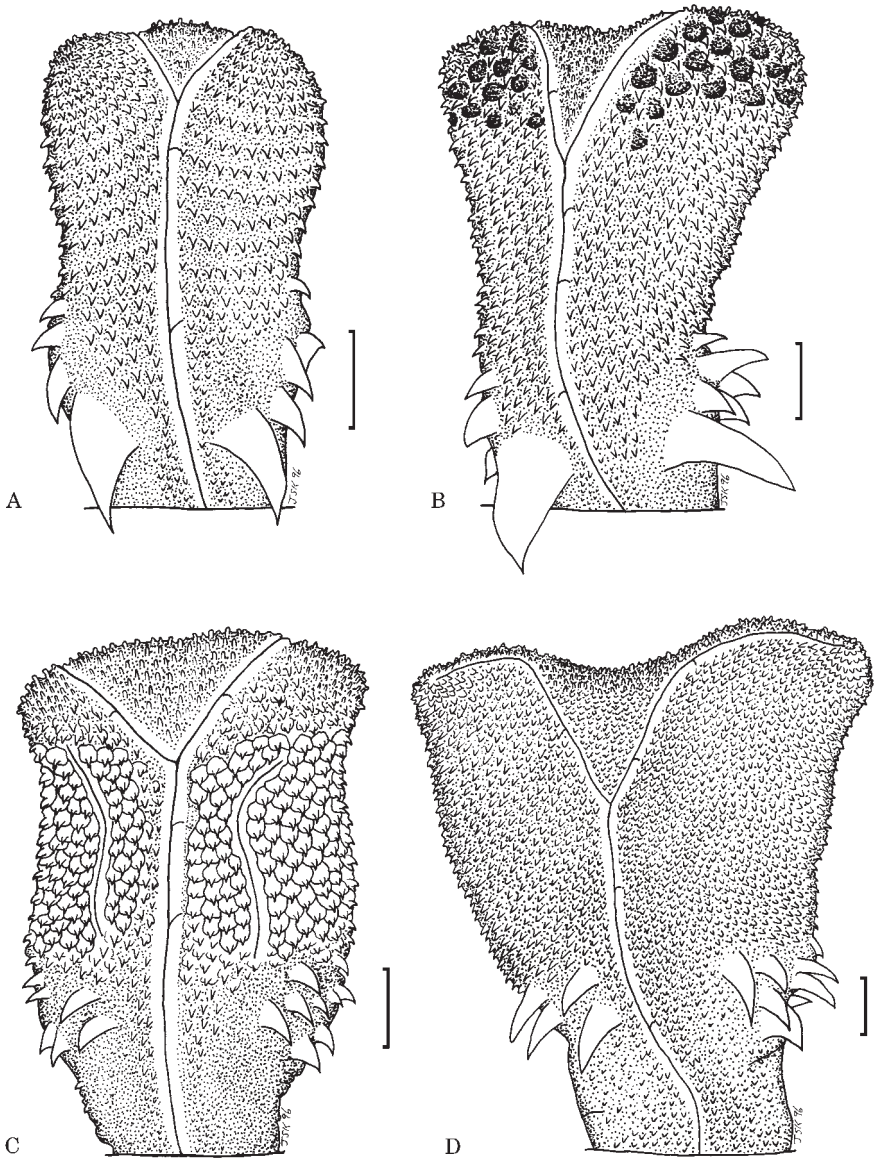

Figure 2. Group 1. Hemipenes of (A) *Demansia atra* (SAM 29954) (B) *Pseudonaja affinis* (SAM 34340) (C) *Pseudechis porphyriacus* (SAM 25056), and (D) *Oxyuranus microlepidotus* (SAM 26876). Scale bars = 3 mm.

Demansia species are united by the bulbous shape of the hemipenis and raised parallel rows of parallel spines.

Pseudonaja. Hemipenes were examined from all seven *Pseudonaja* species. *Pseudonaja* species share a hemipenial shape that is similar to that of *Demansia*, *Pseudechis*, and *Oxyuranus* with a distal flaring of the shallowly-forked apical lobes (compare figures in Fig. 2). However, some intraspecific variation in shape is present; some *P. inframaculata*, *P. ingrami*, *P. nuchalis*, and *P. textilis* specimens display a more 'T' shaped

hemipenis where the apical lobes flare out laterally to a greater extent. However, this morphology did not correlate with any proposed subspecific boundaries and thus appeared to be a real polymorphism in each of these species. Hemipenes of *P. guttata* and *P. modesta* display slightly less differentiated apical lobes. In all species the sulcus divides below the crotch with the apical forks continuing to the tips of the apical lobes. A distinctive spine line is evident in all *Pseudonaja* species and is better expressed on the asulcal surface. Two large basal hooks are present on either side of the sulcus spermaticus, but they are somewhat reduced in *P. guttata* and *P. modesta.* Like *Oxyuranus* and *Pseudechis*, *Pseudonaja* hemipenes are covered in numerous and very small spines. Other types of ornamentation are diverse in *Pseudonaja.* All species except *P. guttata* and some *P. nuchalis* display calyces. Most specimens of all species display ridges but some specimens of *P. inframaculata*, *P. nuchalis*, and *P. textilis* lacked ridges. In these three species plus *P. ingrami* the area between the apical lobes may be covered with calyces and/or ridges that in turn may be spinulate, scalloped, papillate or any combination of these. Thus, a considerable amount of ornamentation variation is present both between and within species. Taking the range of variation into account, it would be very difficult to differentiate among the hemipenes of *P. inframaculata*, *P. ingrami*, *P. nuchalis*, and *P textilis*.

In addition to their unique shape, *Pseudonaja* species are united by the presence of large basal hooks (shared with *Demansia*) and very small spines covering the organ (shared with *Pseudechis* and *Oxyuranus*).

Pseudechis. Hemipenes were examined from *Pseudechis australis*, *P. guttatus*, and *P. porphyriacus*. These *Pseudechis* species share a unique 'hourglass' shape with a proximal lateral bulge, slight medial constriction, and a distal flaring of the shallowly forked apical lobes (Fig. 2C). The apical lobes are less evident in *P. porphyriacus* with only slight apical flaring. The sulcus divides near the crotch with the apical forks emptying at the apical tips. A distinctive spine line is present but comprised of more and smaller spines than *Demansia* and *Pseudonaja* species. In some individuals within each *Pseudechis* species, lateral indentations were observed, but it was not clear if these indentations were genuine or preservation artifacts. *Pseudechis* species are unique in the presence of distinctive fleshy protuberances or 'bumps' on the lateral surfaces that form the bases of spines. These protuberances give the hemipenis a lumpy appearance that is most extreme in *P. australis*. Like *Oxyuranus* and *Pseudonaja*, *Pseudechis* hemipenes are covered with numerous very small spines. More complex forms of ornamentation also are present. *Pseudechis australis* and *P. porphyriacus* display calyces while all species examined displayed ridges on the asulcal surface and between the apical lobes in some individuals. Micro-ornamentation on calyces and ridges is represented only by papillae or small spines.

Pseudechis species are united by the unique 'hourglass' shape of the hemipenis, the presence of fleshy protuberances, and the presence of very small spines covering the organ (shared with *Pseudonaja* and *Oxyuranus*).

Oxyuranus. Hemipenes of both *Oxyuranus microlepidotus* and *O. scutellatus* were examined. The *Oxyuranus* hemipenis is distinctive in shape with the organ being wide and virtually round if viewed from above. Apical lobes are obvious but only weakly differentiated (Fig. 2D). The sulcus spermaticus divides well below the crotch with the sulcal forks continuing to the apical tips. An obvious spine line is present that is more heavily expressed on the asulcal surface. Of all the terrestrial Australian elapids examined, *Oxyuranus* have by far the highest density of spines covering the

hemipenial surface. At first glance the hemipenes look as if they are covered in papillae, but closer examination reveals that each protuberance displays a sharp calcified spine. Calyces ornamented with papillae are found only at the tips of the weakly bilobed apices and are more numerous on the asulcal surface. *Oxyuranus* display lateral ridges ornamented with papillae between the apical lobes.

Oxyuranus species are united by their unique hemipenial shape and the high density of very small spines that cover the organ.

(2) *Simoselaps semifasciatus* and *'Neelaps'*

As currently understood, *Simoselaps* can be divided into three species groups (Shine, 1984a, b): the oophagous *semifasciatus* group with a shovel-shaped rostrum (*S. approximans*, *S. australis*, *S. fasciolatus*, *S. incinctus*, *S. semifasciatus*), the annulate *bertholdi* group with a wedge-shaped rostrum (*S. anomalus*, *S. bertholdi*, *S. littoralis*, and *S. minimus*), and what I call the '*Neelaps*' group in reference to the generic level distinction of some authors who place in *Neelaps* two species with slender bodies and a rounded rostrum (*S. bimaculatus* and *S. calonotus*). I have examined hemipenes from all currently recognized species of *Simoselaps* except *S. littoralis* and *S. minimus*, for which none were available. Members of the *semifasciatus* and *Neelaps* groups share a hemipenial type that is described in this section. Members of the *bertholdi* group which I was able to examine share a very different hemipenial morphology with *Vermicella* (Group 3, see below).

Species in the *S. semifasciatus* and *Neelaps* groups share a hemipenial morphology that is distinct from all other Australian elapids (Fig. 3A, B). Unfortunately, only partially everted hemipenes were available for *S. bimaculatus* so aspects of shape and apical ornamentation could not be ascertained. All members of these two *Simoselaps* species groups posses a cylindrical hemipenial shape that is shallowly forked with distinctly pointed apical lobes. The apical tips may simply point upward or face medially, but orientation of the tips is not species specific (see Fig. 3A, B). The sulcus divides below the crotch with the forks continuing to the apical tips. A spine line is present on the asulcal surface in all members (not shown in Fig. 3A, B), although it is quite weak in *S. approximans*, *S. bimaculatus*, *S. calonotus*, and *S. incinctus*. The spines are fairly sparse and medium sized, though somewhat more numerous on the asulcal surface. No form of more complex ornamentation was found although all species do display numerous papillae on the apical lobes that continue into the crotch (distal end of the hemipenis could not be studied in *S. bimaculatus*). The base is ornamented with small spines in all species except *S. incinctus*. The hemipenis of *S. calonotus* differed slightly from the other members in that it displays a very small papillate medial projection that protrudes from between the apical lobes. It is similar in appearance to the much more prominent medial projection found in the *Rhinoplocephalus–Suta* group but is much smaller.

In addition to the unique shape, members of this group are united by the small and pointed apical lobes.

(3) *Simoselaps bertholdi* and *Vermicella*

As noted above, members of the *S. bertholdi* group examined (*S. anomalus* and *S. bertholdi*) share a unique and distinctive hemipenial morphology with *Vermicella* (*V. annulata* and *V. intermedia* examined, hemipenes of *V. multifasciata*, *V. snelli*, and *V. vermiformis* were unavailable—taxonomy following Keogh and Smith, 1996) and not

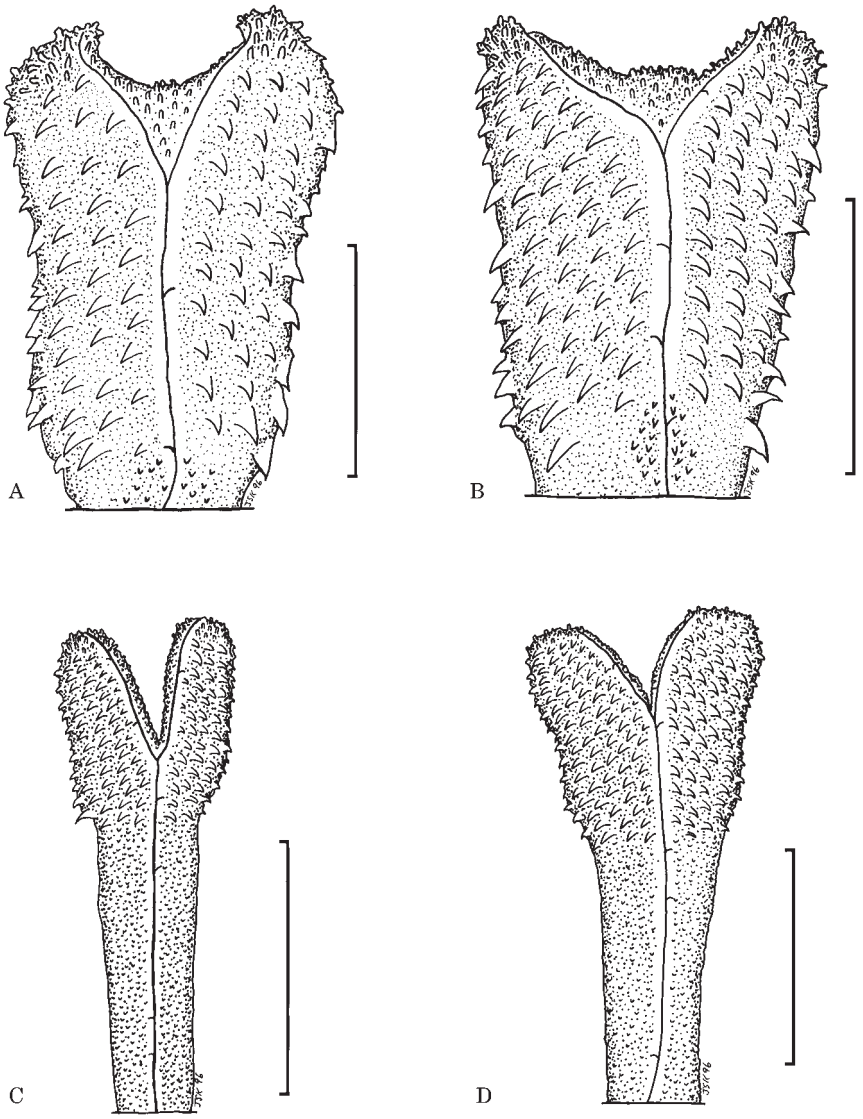

Figure 3. Group 2. Hemipenes of (A) *Simoselaps calonotus* (AM 125365) and (B) *Simoselaps semifasciatus* (SAM 22825). Group 3. Hemipenes of (C) *Simoselaps bertholdi* (SAM 26181), and (D) *Vermicella annulata* (AM 82583). Scale bars = 3 mm.

with other species currently assigned to *Simoselaps* (Fig. 3C, D). The hemipenis is forked with distinct rounded apical lobes. The most obvious aspect of the unique shape is the slender and elongate basal stalk on which the spinose region is perched. The sulcus divides in or just below the crotch with the forks emptying at the apical tips. No spine line is evident. The evenly distributed spinose region is restricted to the distal half of the organ with a distinctive line of demarcation between the basal and distal halves. The long basal portion displays tiny spines on the sulcal surface that gradually diminish toward the base. No complex forms of ornamentation are

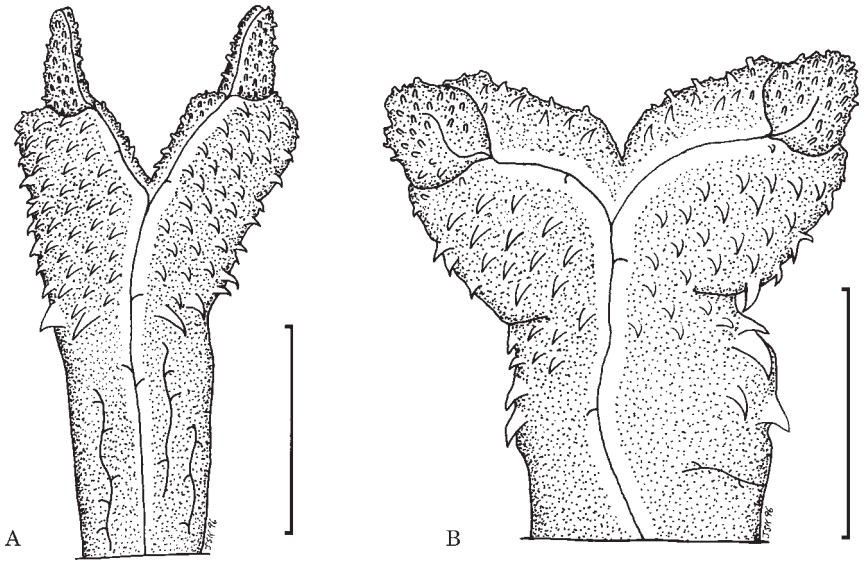

Figure 4. Group 4. Hemipenes of (A) *Cacophis squamulosus* (QM 26352) and (B) *Furina ornata* (SAM 26885). Scale bars = 3 mm.

evident although a small number of apical papillae are present in all species examined except *S. bertholdi*.

Members of this group are united by the presence of an elongate basal stalk (shared with *Cacophis* and *Furina*), sharp line of demarcation between the basal and spinose regions, and the forked and rounded apical lobes (shared with *Cacophis* and *Furina*).

(4) *Cacophis* and *Furina*

Hemipenes were examined from *Cacophis squamulosus*, *Furina diadema*, *F. dunmalli*, *F. ornata*, and *F. tristis* and they share a unique hemipenial shape (Fig. 4A, B). The organ is distinctly forked with long apical lobes and a long, thin basal portion up to half the total length of the organ, giving the hemipenis the appearance of being at the end of a stalk. Each apical lobe is constricted at approximately mid-point by a lip that divides the proximal section of the apical lobes from the thinner projecting terminal awns. The sulcus divides in or just below the crotch with the forks terminating at the tips of the terminal awns. Ornamentation is relatively simple. A spine line is present but very weak in all species examined. The basal portion of the organ is nude while the distal half of the hemipenial surface is sparsely covered with medium to large sized spines that diminish in size near the sulcal surface of the base. The terminal awns are covered with numerous small papillae. Only the single specimen available of *F. tristis* displays slightly more complex ornamentation with papillate and spinulate ridges on the asulcal surface.

Cacophis and *Furina* are united by the presence of a long basal stalk (shared with *Simoselaps bertholdi* group and *Vermicella*), forked apical lobes with terminal awns, and a nude base (shared with *Rhinoplocephalus* and *Suta*).

(5) *Austrelaps*, *Echiopsis*, *Hoplocephalus*, *Notechis* and *Tropidechis*

Before describing hemipenial morphology in this group, it is necessary to make some taxonomic comments regarding *Austrelaps* and *Notechis* as they relate to hemipenial variation. Until recently, *A. superbus* has been regarded as a monotypic genus with subspecies *A. s. superbus*, *A. s. ramsayi*, and *A. s. labialis* that correspond to what have been referred to as the lowland, highland, and pygmy copperheads, respectively (Shine, 1987a; Cogger, 1992). Similarly, *Notechis scutatus* has been regarded as a monotypic genus with subspecies *scutatus* and *ater* (Cogger, 1992). Rawlinson (1991) elevated the subspecies of *Austrelaps* and *Notechis* to specific status based on subtleties of colour and differences in adult size (for *Austrelaps*), and colour and slight scales count differences (for *Notechis*), though noting unpublished data that suggested that *Notechis* was a single species (Schwaner in Rawlinson, 1991). Though following Rawlinson's (1991) scheme for *Notechis*, Cogger (1992) noted its apparent arbitrariness and did not follow Rawlinson's arrangement for *Austrelaps*. For the purposes of this paper, I treat *Austrelaps* and *Notechis* as 'species complexes' which is appropriate as variation in hemipenial morphology within both genera is small and more importantly, does not correlate with proposed specific or subspecific boundaries.

Hemipenes were available from all members of the group except *Echiopsis atriceps*, known from only five specimens, or *Hoplocephalus bitorquatus*. In all species of this group examined, the hemipenis is shallowly forked with distinctive apical lobes that terminate in pointed and (usually) medially facing tips (Fig. 5). Some apical lobe variation was detected in the *Notechis* complex (for which there was a large sample size of 85 hemipenes) with some individuals showing more strongly bilobed organs. However, this variation did not fall along any proposed specific lines and instead seems to simply reflect real individual variation. For example, the intergeneric differences that can be seen in Figure 5 reflects variation also found within species. The sulcus bifurcates below the crotch with the sulcal forks continuing to the apical tips. A strong and distinctive spine line adorns the hemipenis and may expand to several rows of quite large and numerous spines on the asulcal surface in all members except *Austrelaps* that displays a weak spine line. Spine size over the rest of the organ shows interspecific variation. *Austrelaps*, *Notechis* and *Tropidechis* display quite small spines, while *E. curta* and *Hoplocephalus* display medium sized spines. The spines of *Notechis* and particularly *Austrelaps* are in a slightly higher concentration than in the other members of the group. The base of the organ is ornamented with small spines that diminish in size toward the base. Papillate and spinulate calyces are found on the sulcal and asulcul surfaces of the apical lobes only in *Austrelaps* and a few *Notechis* specimens. However, in these *Notechis* specimens calyces are very weak with the cup-shaped depression only just perceptible. *Austrelaps*, some *Notechis*, and some *Echiopsis* display numerous large and loosely arranged papillate calyces between sulcal forks on the apical lobes (see *Austrelaps* in Fig. 5D). All members of this group display numerous apical papillae.

In addition to their unique shape, *Austrelaps*, *Echiopsis curta*, *Hoplocephalus*, *Notechis*, and *Tropidechis* are united by the pointed and medially facing apical lobes (some specimens of the *Simoselaps semifasciatus* group display medially facing tips [Fig. 3A] but this feature shows intraspecific variation in these species) and a strong spine line (shared with *Demansia*, *Hemiaspis*, some *Pseudonaja* and some *Rhinoplocephalus*).

(6) *Drysdalia* and *hemiaspis*

Hemipenes were available from each of the four *Drysdalia* species and both *Hemiaspis* species. These six species share a relatively simple cylindrical hemipenis

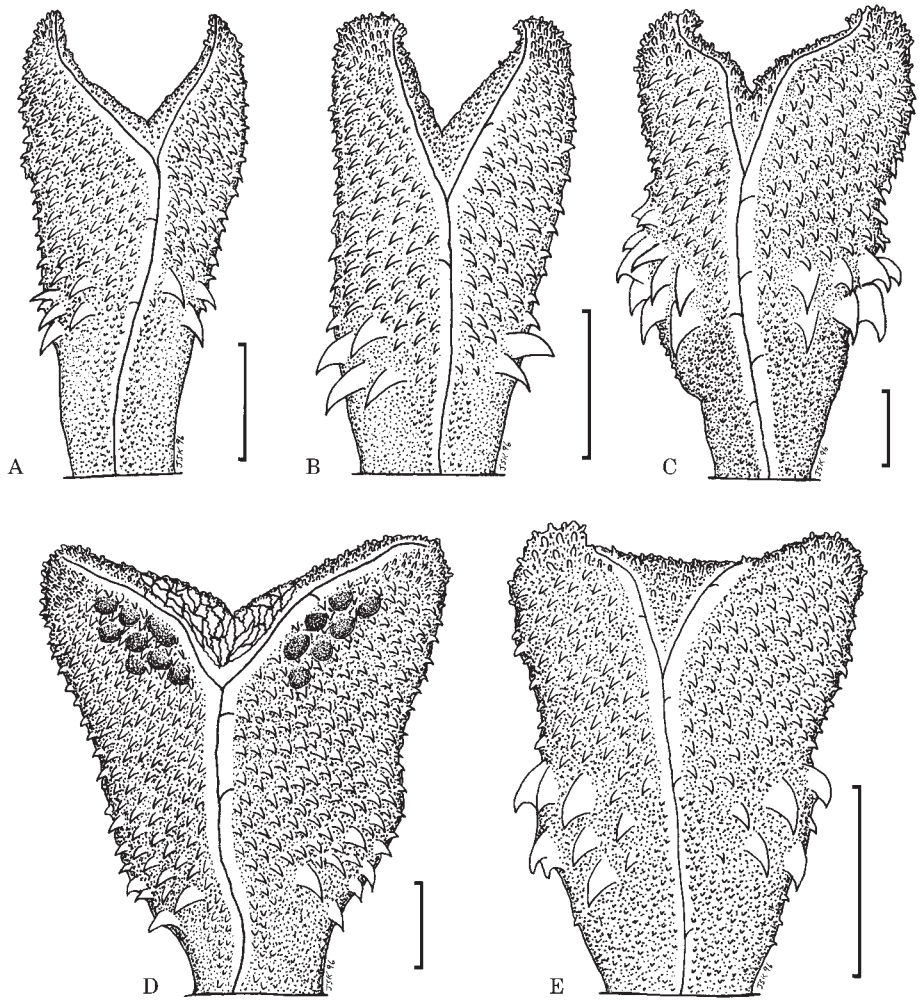

Figure 5. Group 5. Hemipenes of (A) *Tropidechis carinatus* (QM 30435), (B) *Hoplocephalus stephensi* (AM 58516), (C) *Notechis scutatus* (SAM 22949), (D) *Austrelaps superbus* (SAM 21440), and (E) *Echiopsis curta* (SAM 22971), Scale bars = 3 mm.

with only weakly differentiated apical lobes (Fig. 6A, B). The sulcus spermaticus bifurcates near the top of the hemipenis with the sulcal forks continuing a short distance to the top of the apical lobes. An obvious spine line is present (particularly strong in *H. signata*) and is stronger on the lateral and asulcal surfaces, covering up to one half the total length of the asulcal surface. Ornamentation shows interspecific variation. *Drysdalia coronoides*, *D. rhodogaster*, and *H. signata* display spinulate calyces that cover much of the asulcal surface and papillate calyces on the apical lobes. Calyces are lacking in the other species. All species display medium sized spines that cover much of the hemipenis, and papillae on the apical lobes and between the sulcal forks. The spines of *H. signata* are arranged in fairly regular and parallel rows.

Drysdalia and *Hemiaspis* are united by the cylindrical shape of the hemipenis (which

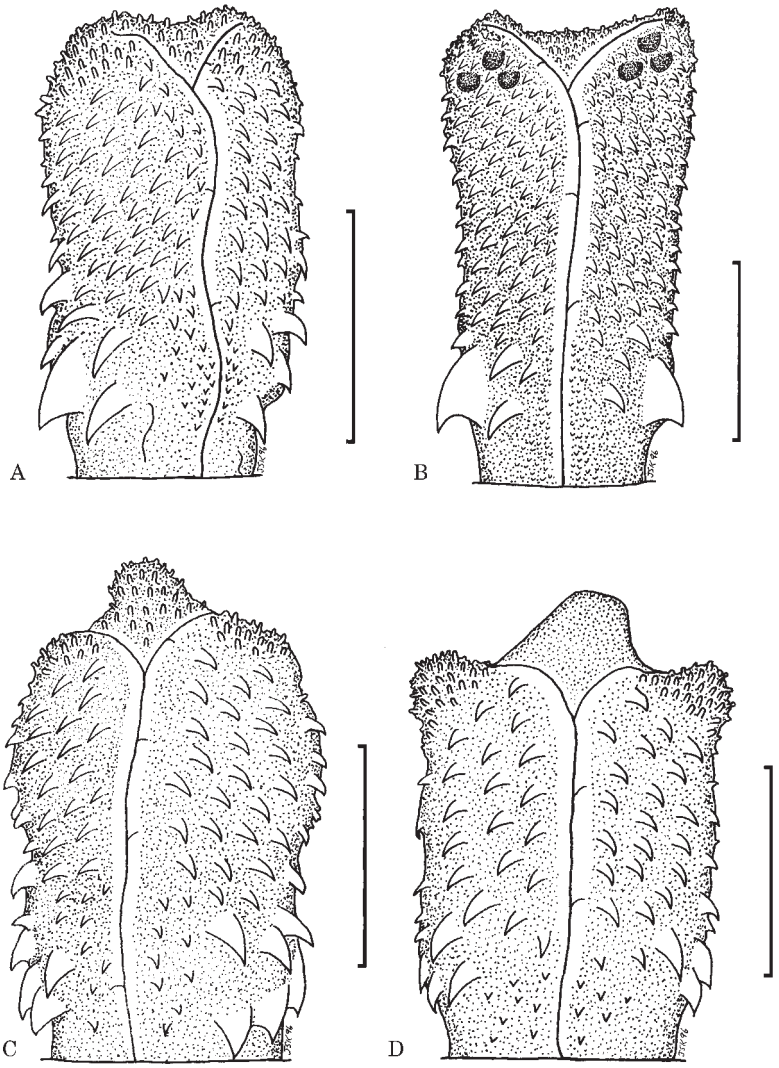

Figure 6. Group 6. Hemipenes of (A) *Drysdalia mastersi* (SAM 21956) and (B) *Hemiaspis signata* (VIC 15311). Group 7. Hemipenes of (C) *Rhinoplocephalus nigrescens* (SAM 23172) and (D) *Suta spectabilis* (SAM 22484). Scale bars = 3 mm.

lacks a medial projection as seen in *Rhinoplocephalus* and *Suta*) and the weakly differentiated apical lobes (shared with *Rhinoplocephalus* and *Suta*).

(7) *Rhinoplocephalus* and *Suta*

Hemipenes were available for four of the five currently recognized *Rhinoplocephalus* species (*R. pallidiceps* unavailable) and all nine *Suta* species (I follow Cogger in treating *dwyeri* as a subspecies of *S. spectabilis*) which share a unique hemipenial morphology (Fig. 6C, D). Like *Drysdalia* and *Hemiaspis*, the hemipenis is cylindrical with only very weakly differentiated apical lobes. The sulcus spermaticus bifurcates at the base of the medial projection and the forks transverse the short distance to the tips of the

apical lobes. All species lack distinct basal hooks yet they all posses an obvious spine line that displays interspecific differences in expression (strong in *R. bicolor*, *R. nigrescens*, *S. gouldi*, *S. monachus*, *S. nigriceps*, *S. ordensis*, and *S. suta*; weak in *S. fasciata*, *S. flagellum*, *S. punctata*, and *S. spectabilis*). *Rhinoplocephalus* and *Suta* are unique in their possession of a large medial projection that protrudes from between the sulcal forks and thus the apical lobes. In some specimens the projection was quite bulbous, but this appeared to be an artifact of over-inflation at the time of preservation as in these specimens the entire hemipenis appeared especially turgid. Only *Simoselaps calonotus* displays a similar medial projection, but it is much smaller and may not be homologous. Ornamentation of the medial projection is variable both between and within species. In all specimens of *R. boschmai*, *S. gouldi*, *S. monachus*, and *S. spectabilis* examined, the medial projection is nude and smooth while the apical lobes are papillate (except for *S. monachus* that displays nude smooth apical lobes). However, the medial projections of *R. bicolor*, *R. nigrostriatus*, *S. flagellum*, *S. nigriceps*, *S. ordensis*, and *S. punctata* display some degree of papillate ornamentation. *Rhinoplocephalus nigrescens* displays both papillae and small spines on the medial projection. The hemipenes of *S. fasciata* and *S. suta* show a great deal of variability. Within each species both the apical lobes and medial projection may be nude, papillate, spinulate or any combination of these. However, I suspect that this variability may not mean much as larger sample sizes would probably reveal widespread variability. The *Rhinoplocephalus–Suta* clade displays no complex ornamentation. The hemipenis is simply covered with medium sized spines. The base of the hemipenis is nude although spines on the sulcal surface may continue to the base at a diminished size in some specimens.

Rhinoplocephalus and *Suta* are united by presence of a large medial projection, nude base (shared with *Cacophis* and *Furina*), and weakly differentiated apical lobes (shared with *Drysdalia* and *Hemiaspis*).

(8) *Acanthophis* and *Denisonia*

Acanthophis. Hemipenes were examined from *Acanthophis antarcticus* and *A. praelongus* which share a hemipenial type (Fig. 7A). The organ is deeply forked, with each perfectly cylindrical apical lobe ending in a flat apical disk that is devoid of any ornamentation and covered with smooth epithelium. However, some specimens displayed a small medial projection on each lobe (Fig. 7A) (not *between* the lobes as in *Rhinoplocephalus* and *Suta*). The sulcus spermaticus bifurcates just below the crotch and continues along the medial surfaces of the apical lobes, through the edges of the thick lips of the apical disks and empties onto the disk centre. *Acanthophis* displays no obvious spine line, and no forms of complex ornamentation are evident. The hemipenis is sparsely covered with medium sized spines that become gradually smaller toward the base. The single *A. praelongus* specimen studied had a completely nude base.

Acanthophis species are united by the cylindrical and deeply forked apical lobes and apical disks.

Denisonia. Everted hemipenes were available from *Denisonia devisi* but dissected organs of the sister species *D. maculata* also were examined. *Denisonia devisi* displays a distinctly forked hemipenis with two very round, bulbous apical lobes (Fig. 7B). Dissections of three museum specimens revealed that *D. maculata* also shares the strongly forked

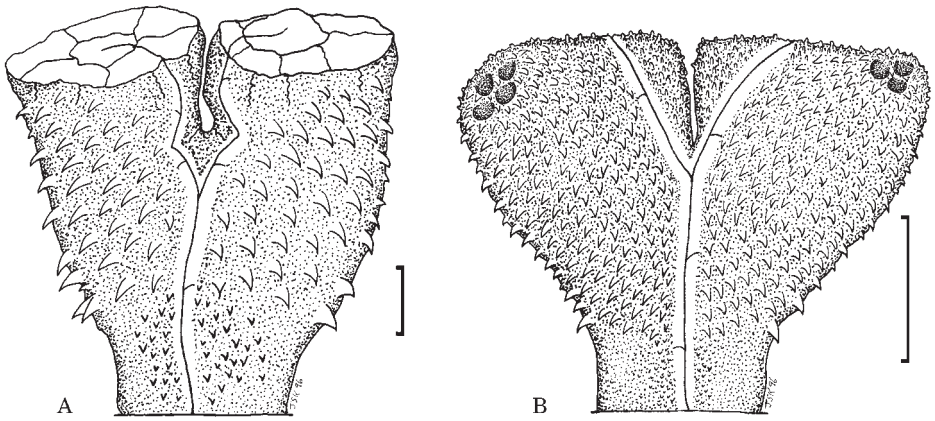

Figure 7. Group 8. Hemipenes of (A) *Acanthophis antarcticus* (SAM 30497) and (B) *Denisonia devisi* (QM 5888). Scale bars = 3 mm.

hemipenial shape. The sulcus spermaticus divides in or just below the crotch and continues up either the inner side or outside of the hemipenis to empty at the lateral edges of the apical lobes. Though lacking the terminal disks of *Acanthophis*, the top surface of the apical lobes in *Denisonia* are flat and covered with parallel rows of papillae and raised papillate ridges medially, and papillate and spinulate calyces laterally that continue onto the asulcal surface and around the lateral edge of the apical lobes where the sulcus spermaticus drains. A spine line is present but weak and the spines covering the rest of the hemipenis are medium sized and arranged in fairly regular parallel rows.

Denisonia species are united by the large, rounded, bulbous apical lobes with a flat distal surface.

DISCUSSION

It has been argued that copulatory organs differ from other organ systems in their ability to retain changes through evolutionary time and thus are inherently more stable than many other morphological systems used in systematic assessment (Arnold, 1983, 1986a, b). Arnold (1986b) outlined a number of features of squamate reptiles that might promote stability in hemipenial characters: (i) the hemipenes are internal structures and thus less likely to be affected by the strong selective forces acting on external morphological characters; (ii) there is only a single known function, thus one would predict fewer selective forces; (iii) hemipenial morphology is probably unaffected by changes in niche, in contrast to other body parts, and (iv) individual males should posses hemipenes that are compatible with the morphology of as many females as possible within the local population, so any incompatibilities would be strongly selected against. Because of this apparent stability, hemipenial characters have proven to be excellent indicators of relationship (Cope, 1895; Dowling & Savage, 1960; Arnold, 1973, 1983, 1986a, b), and it has generally been the case that where copulatory organ morphology has suggested either a close or distant

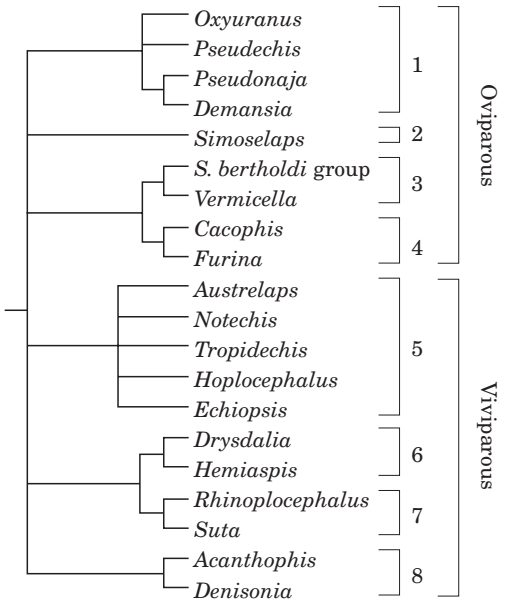

Figure 8. Summary of the phylogenetic implications of hemipenial morphology in the terrestrial Australian elapid snakes. Numbers refer to the hemipenial groups used in this paper. The nodes shown are only those supported by synapomorphies drawn from hemipenial morphology. I display the oviparous and viviparous groupings because other authors have found reason to support the naturalness of these groups within the terrestrial Australian elapids, although hemipenial morphology neither supports nor refutes these higher level groupings.

relationship between taxa, further studies based on other data sets have been confirmatory (Arnold, 1986a, b).

Hemipenial morphology in the terrestrial Australian elapids tends to be highly conservative at supraspecific levels with hemipenial types shared among species (Fig. 8). Moreover, for the majority of cases, these groupings are largely supportive of previously suggested hypotheses of higher level relationships and taxonomic lines among Australian elapids based on data sets as diverse as chromosomes, soft anatomy, electrophoresis, ecology, immunological distance, venom proteins and DNA sequences (Fig. 9). Corroboration of results from different data sets is thought to be the most convincing evidence for relationship among taxa (Bailey, 1967; Underwood, 1967b). I acknowledge that some groups may be based partially on plesiomorphic hemipenial characters. However, I contend that this is a minimal occurrence because the weight of corroborating evidence, at least in terms of identifying putative monophyletic clades, suggests that most of my hemipenial groupings are probably real. Thus, I interpret these hemipenial 'types' as indicative of relationship and natural groups except where stated otherwise. As stated previously, these same data will be incorporated into a fully cladistic analysis with other morphological data sets. Below I discuss the composition of each of the hemipenial groupings in relation to past work.

Demansia, *Pseudechis*, *Pseudonaja* and *Oxyuranus*

Demansia species form a well defined clade, and their generic level status has been stable since the splitting of these species from *Pseudonaja* by Worrell (1961). *Demansia*

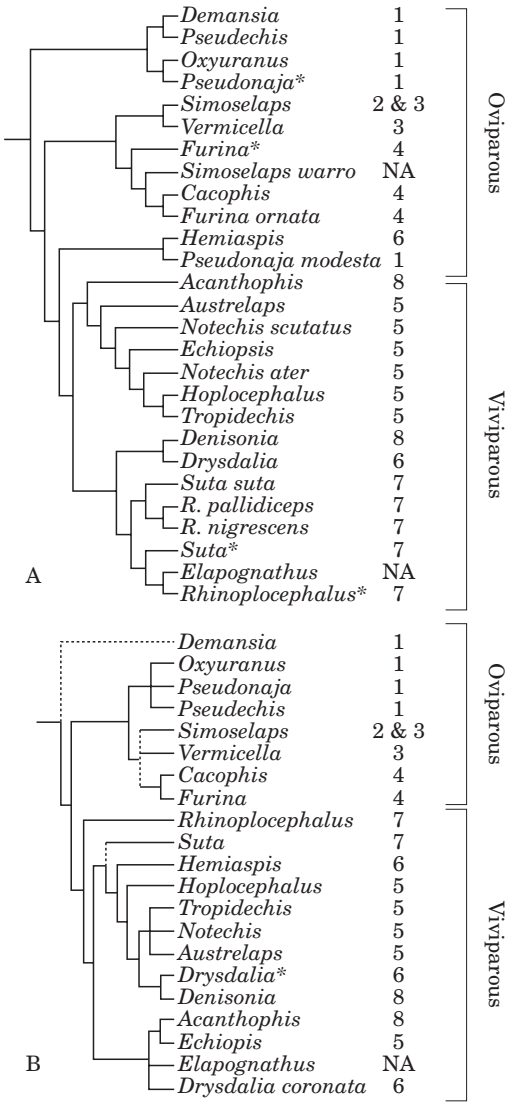

Figure 9. Previous phylogenetic hypotheses for the terrestrial Australian elapid snakes and their congruence with hemipenial morphology. A, morphologically based phylogeny of Wallach (1985). B, electrophoretic and karyologically based phylogeny of Mengden (1985a). Numbers refer to hemipenial groups used in this paper. Each tree has been re-drawn to incorporate the classification scheme of Hutchinson (1990). Hemipenes from *Simoselaps warro* and *Elapognathus minor* were not available for examination (NA). Hemipenial morphology is largely supportive of groupings found by these authors.

species are among the most distinctive members of the terrestrial Australian elapid fauna, with a relatively long tail, slender body and slight build, large eyes, and 15 dorsal scale rows (Cogger, 1992). Monophyly of this highly derived clade is supported by morphological (Wallach, 1985) and karyological evidence (Mengden, 1985) and is further corroborated by the unique nonlobate and bulbous hemipenis with uniform parallel rows of spines and enlarged basal hooks shared by the members of this

genus. However, while hemipenial synapomorphies clearly unite the *Demansia* species examined, it does not shed light on intrageneric relationships.

The seven *Pseudonaja* species form a well-defined genus based on morphological (Worrell, 1961; Wallach, 1985), electrophoretic and karyological data (Mengden, 1985a, b). *Pseudonaja* monophyly is further corroborated by unique hemipenial synapomorphies. Mengden (1985a) found that *Pseudonaja* species formed a karyomorph group distinct among terrestrial Australian elapids with *Pseudonaja affinis*, *P. guttata*, *P. ingrami*, *P. modesta*, and *P. textilis* each displaying unique re-arrangements while *P. nuchalis* morphs display three unique re-arrangements (Mengden, 1985b). Indeed, *Pseudonaja* displays more intrageneric variation than any other elapid genus and a larger range of diploid numbers and chromosomal re-arrangements than any other genus of snake studied to date (Mengden, 1985b). While hemipenial morphology clearly unites *Pseudonaja* species, it does not elucidate relationships within the genus. The large sample of *P. textilis* hemipenes examined from throughout the range (77) revealed some variation in spine density and apical lobe shape. However, this variation did not correspond to any specific populations and instead represents individual variation. This is consistent with karyotype data (Mengden, 1985b) and does not support the distinctiveness of populations identified by Gillam (1979). However, some of eight distinct *P. nuchalis* colour morphs (Gillam, 1979) have unique karyotypic re-arrangements (Mengden, 1985b) supporting the notion that the species is composite (Mengden, 1985b; Cogger, 1992). Examination of 56 *P. nuchalis* hemipenis from a number of the proposed colour morphs revealed that hemipenial morphology is conservative in *P. nuchalis*. While variation in hemipenial morphology was found, particularly in shape of the apical lobe (as for *P. textilis*), this variation did not correlate with proposed morph boundaries, and thus is not useful to address the proposed composite nature of *P. nuchalis*. While not useful intra-specifically, hemipenial morphology unambiguously unites *P. modesta* with its congeners rather than *Hemiaspis* species as suggested by morphological data (Wallach, 1985), a finding corroborated by data on karyotypes (Mengden, 1985b) and mitochondrial DNA sequences (Keogh *et al.*, 1998). Lastly, it is worth noting that Mengden (1985b) found that *P. guttata* displayed the greatest genetic distance from its congeners based on electrophoretic data. *Pseudonaja guttata* is also slightly divergent from other *Pseudonaja* in hemipenial morphology.

The six currently recognized species of *Pseudechis* form a monophyletic group and several lines of evidence suggest that they are closely related. Indeed their generic level status has been stable since the work of Mackay (1955). Hemipenial morphology unambiguously supports *Pseudechis* monophyly, including the viviparous *P. porphyriacus*, with all members sharing a unique shape and the presence of distinctive fleshy protuberances on the outside of the organ. Other data sets have demonstrated that while *Pseudechis* species are probably monophyletic, intra-generic divergences may be quite ancient. For example, *P. porphyriacus* is closest to its congeners *P. butleri* and *P. colletti* in immunological distance, but not especially close (Schwaner *et al.*, 1985) and *Pseudechis australis*, *P. porphyriacus*, and *P. guttatus* did not always form a monophyletic group in Wallach's (1985) morphological study. Wallach attributed this result to the high number of plesiomorphic characters found in the genus. A detailed study of *Pseudechis* relationships based on characters drawn from cytogenetics, scalation, external morphology, and electrophoretic patterns clearly demonstrated *Pseudechis* monophyly although *P. porphyriacus* is quite distinct (Mengden *et al.*, 1986). The

distinctiveness of this species is also supported by mitochondrial DNA sequence data (Keogh *et al.*, 1998).

Until the revision of *Oxyuranus* by Covacevich *et al.* (1981), the genus was monotypic, with only the taipan, *O. scutellatus*, recognized. *Oxyuranus microlepidotus* previously had been variously referred to *Pseudonaja*, *Pseudechis*, *Oxyuranus*, and most recently as the monotypic *Parademansia* (see Covacevich *et al.*, 1981). Their case for inclusion of both species in an expanded *Oxyuranus* was convincing with evidence drawn from external morphology, cranial osteology, dentition, head musculature, venom characteristics, hemipenial morphology, karyotypes, and aspects of behaviour. Fohlman (1979) earlier had suggested that the two species were congeneric based solely on venom composition. In addition, both species are ecologically very similar in a number of aspects, most notably in their specialization on mammalian prey (Shine & Covacevich, 1983; Shine, 1985). Hemipenial morphology of *Oxyuranus* clearly supports the earlier notion that *O. scutellatus* and *O. microlepidotus* are sister species and deserving of congeneric status. Covacevich *et al.* (1981) published photographs of the hemipenes of both species stating that the organs were similar in that they were moderately long, narrow, and simple, and noted the following differences ". . . proximal to the distal spinulose zone, there are more irregular transverse whorls of enlarged spines, fewer in '*Parademansia*' than in *Oxyuranus* (1 vs. 3). Further, the small spines on the distal part of the organ of '*Parademansia*' are evenly spaced, but in *Oxyuranus* are arranged in groups of 3–5". They did not mention the sample size used in their assessment of hemipenial variation, but it is worth noting that the differences outlined by Covacevich *et al.* (1981) were found to be well within the normal range of variation found in both species. Indeed, when this variation is taken into account, hemipenial morphology of *O. scutellatus* and *O. microlepidotus* is virtually indistinguishable and moreover, is different enough from the other members of this group to be highly identifiable.

The hemipenes of *Oxyuranus*, *Pseudechis*, *Pseudonaja*, and *Demansia*, though each unique, share certain features in common. The overall shape of the organ is shared among the group, but all members also possess a distinctive line of demarcation between the spine line and the spines that cover the more distal part of the organ. In addition, the hemipenes of *Oxyuranus*, *Pseudechis*, and *Pseudonaja* are covered with very small spines that also are found in a much greater density than in all other terrestrial Australian elapid groups. While *Pseudonaja*, *Pseudechis*, and *Oxyuranus* have been thought to be each others' closest relatives based on morphological (Worrell, 1961; McDowell, 1967; Wallach, 1985), cytogenetic and electrophoretic (Mengden, 1985a, b; Mengden *et al.*, 1986) and immunological distance data (Schwaner *et al.*, 1985), the phylogenetic position of *Demansia* has be somewhat more difficult to ascertain. *Demansia* species are immunologically highly divergent from other Australian elapid species (Cadle & Gorman, 1981; Mao *et al.*, 1983; Schwaner *et al.*, 1985), and not only possess a karyomorph unique among the Australian elapids, but also one that is not easily derived from or associated with the others (Mengden, 1985a). Despite this strong evidence for a more distant relationship of *Demansia* to other Australian elapids, this result is not supported by mitochondrial DNA sequence data (Keogh, 1998; Keogh *et al.*, 1998) or by my data on hemipenial morphology. In particular, although *Demansia* and *Pseudonaja* each possess distinct hemipenial morphologies, their copulatory organs are very similar in shape, ornamentation, and most convincingly, in the presence of two very enlarged basal hooks. Indeed, similarities between the organs of the larger *Demansia* species (*D. atra* and *D. papuensis*)

and *Pseudonaja* hemipenes are so striking that they are virtually indistinguishable except for the presence of the very regular rows of parallel spines in *Demansia*. These contradictory data could be interpreted in several ways. It may be that *Demansia* are immunologically more quickly evolving than their Australian relatives (a possibility noted by Cadle & Gorman, 1981). The possibility also exists that *Demansia* may be more closely related to some other elapid group. For example, *Demansia* has been associated with the New Guinea genus *Aspidomorphus* (McDowell, 1967; Keogh *et al.*, 1998). If this is this case, *Demansia* and *Pseudonaja* may have converged on highly similar hemipenial morphologies, or, if *Demansia* and the other group members are derived from the same ancestral stock, this general hemipenial shape and possibly the presence of enlarged basal spines simply may be the plesiomorphic condition. Wallach (1985) and Mengden (1985a, b) both found these genera to be basal relative to the rest of the Australian elapid radiation.

Simoselaps, '*Neelaps*' and *Vermicella*

The members of *Simoselaps* and *Vermicella* have long been thought to be closely related. As defined by Hutchinson (1990), *Simoselaps* is comprised of several distinct subgroups defined by both morphological and ecological specialization. These subgroups have been variously treated taxonomically (Storr, 1967, 1979; Shine, 1984a, 1985; Scanlon, 1985; Wallach, 1985; Scanlon & Shine, 1988; Cogger, 1992; Keogh & Smith, 1996). This genus of small, banded, fossorial snakes is currently comprised of (i) the oophagous *semifasciatus* group with a shovel-shaped rostrum (*S. approximans*, *S. australis*, *S. fasciolatus*, *S. incinctus*, *S. semifasciatus*) which feed primarily or exclusively on the eggs of other reptiles, (ii) the annulate and primarily scincid lizard eating *bertholdi* group with a wedge-shaped rostrum (*S. anomalus*, *S. bertholdi*, *S. littoralis*, and *S. minimus*), and (iii) the scincid lizard eating *Neelaps* group, with slender bodies and a rounded rostrum (*S. bimaculatus* and *S. calonotus*). *Vermicella* is comprised of five species united by, among other things, a pattern of alternating black and white bands, an elongate cylindrical body, 15 dorsal scale rows, divided anal plate and subcaudal scales, and a short blunt tail (Keogh & Smith, 1996). However, as noted above, though *Vermicella* appears morphologically well defined, other authors have found reason to recognize an expanded *Vermicella*. In particular, Storr's (1967, 1979) concept of *Vermicella* includes *Simoselaps* as currently understood.

Clearly, the phylogenetic relationships and generic boundaries of this group are problematical. Hemipenial morphology provides evidence for both the unification of some members of *Simoselaps* (including those species sometimes assigned to *Neelaps*) and the separation of the *Simoselaps bertholdi* group that instead share synapomorphies with *Vermicella*. The 'sand-swimming', oophagous *S. semifasciatus* group is morphologically well defined, although the placement of the *Neelaps* group has been more difficult as these two species display a somewhat different body shape. They are elongate and slender (particularly *S. bimaculatus*) relative to the *S. semifasciatus* group, a feature they share with *Vermicella*. However, rather than supporting a *Neelaps–Vermicella* clade (as suggested by Wallach [1985] and Scanlon [1985]), hemipenial morphology unites the *Neelaps* group (*S. calonotus* and presumably *S. bimaculatus*) with the 'sand-swimming' *Simoselaps semifasciatus* group to the exclusion of the *S. bertholdi* group–*Vermicella* clade (*contra* Mengden, 1985a). Given the strong hemipenial evidence, it is worth noting that only *Vermicella* and members of the *S. bertholdi* group, alone among *Simoselaps*, display a distinctive alternating banded

pattern. The *S. bertholdi* group also displays a unique karyotype among the terrestrial Australian elapids (Mengden, 1985a). Despite the strong evidence for a natural grouping of *Vermicella* and the *S. bertholdi* group, mitochondrial DNA sequence data have supported a closer grouping between *S. bertholdi*, *S. semifasciatus*, and *S. bimaculatus*, to the exclusion of both *S. calonotus* and *Vermicella* (Keogh *et al.*, 1998). It is clear that *Simoselaps* as currently understood is paraphyletic (Mengden, 1985a; Cogger, 1992), but given the contradictory evidence for where taxonomic lines of demarcation can be drawn, redefining *Vermicella* to include the *S. bertholdi* group would be premature. Lastly, it is worth noting that the *S. bertholdi–Vermicella* hemipenial type is actually much more similar to that of *Cacophis–Furina* than to the other members of *Simoselaps*.

Cacophis and *Furina*

The generic status of species now included in *Cacophis* and *Furina* has been somewhat convoluted, with *Cacophis* species previously assigned to *Aspidomorphus*, and *Furina* species split into *Glyphodon* (for *F. barnardi*, *F. dunmalli*, and *F. tristis*) and *Furina* (for *F. ornata* and *F. diadema*). Based on hemipenial morphology, dentition, head scalation and colour patterns, McDowell (1967) allocated the Australian *harriettae*, *kreffti*, and *squamulosus* to *Cacophis*, to emphasize their distinctiveness from the New Guinea *Aspidomorphus lineaticollis*, *A. muelleri*, and *A. schlegeli*. He considered *Aspidomorphus* to be more closely related to *Demansia* (a relationship also supported by mitochondrial DNA sequence data [Keogh *et al.*, 1998]). Whatever the relationships of *Aspidomorphus*, the close relationship of species now included in *Cacophis* and *Furina* has long been suspected (McDowell, 1967) and is supported by more recent morphological data sets (Wallach, 1985). Schwaner *et al.* (1985) grouped *Cacophis* and *Furina* together based on immunological distance, but this group also included other diverse genera such as *Denisonia*, *Drysdalia*, *Vermicella* and *Oxyuranus* (from their figure 4). The close relationship of *Cacophis* and *Furina* is strongly supported by hemipenial synapomorphies that unambiguously unite the members of these genera to the exclusion of all other terrestrial Australian elapids. In particular, the forked hemipenis displays distinct apical lobes with terminal awns, a feature not observed in any other Australian elapid group. It also is worth noting the strong ecological similarities of *Cacophis* and *Furina* (Shine, 1980a, 1981a).

Although the *Cacophis–Furina* clade and the *Simoselaps bertholdi* group–*Vermicella* clade each display unique hemipenial morphologies, these groups also share strong hemipenial characteristics (compare Figs 3C, D and 4A, B). Both groups display a hemipenis with a long basal stalk, strong well separated apical lobes, and ornamentation primarily on the distal half of the organ. The only significant difference between the hemipenial types is the additional terminal awns displayed by *Cacophis* and *Furina*. Close associations between *Cacophis* and *Furina* on the one hand and *Vermicella* and *Simoselaps* members on the other hand are supported by other data sets (Wallach, 1985; Mengden, 1985a; Schwaner *et al.*, 1985).

Austrelaps, *Echiopsis*, *Hoplocephalus*, *Notechis* and *Tropidechis*

Hemipenial morphology provides evidence that *Austrelaps*, *Echiopsis*, *Hoplocephalus*, *Notechis*, and *Tropidechis* are closely related. All members share a unique hemipenial type, which is virtually indistinguishable among these taxa. The close relationship of these genera is corroborated by other morphological data sets (i.e. Storr, 1982; Wallach, 1985). Further, *Austrelaps*, *Notechis*, and *Tropidechis* share a karyomorph type

unique among the terrestrial Australian elapids, and also are electrophoretically close (Mengden, 1985a). *Hoplocephalus* species share a unique karyomorph type, but one that Mengden (1985a) could derive from the *Notechis* group (as implied by his figure 2). The very close relationship of some (*Austrelaps* and *Notechis*—Minton & da Costa, 1975) or all of these genera (Schwaner *et al.*, 1985) is strongly supported by immunological distance data. Moreover, there are strong ecological similarities among members of this group (Shine & Charles, 1982; Shine, 1985, 1987a, b). Although, some diverse data sets have supported the hypothesis that *E. curta* may be more closely related to *Acanthophis* than to the *Notechis* lineage (Marshal & Herrman, 1984; Mengden 1985a; Keogh *et al.*, 1998), hemipenial morphology unites *E. curta* with the *Notechis* lineage and not *Acanthophis*, a finding that is in agreement with the morphological data sets of Storr (1982) and Wallach (1985) and the immunological data of Schwaner *et al.* (1985). Though hemipenial morphology is highly divergent between the other members of this group (including *Echiopsis*) on the one hand and *Acanthophis* on the other (compare Figs 5D and 7A), the contradictory evidence indicates that the affinities of *Echiopsis* require further attention.

Drysdalia and *Hemiaspis*

Hemiaspis dameli and *H. signata* superficially are not especially similar-looking snakes. They display somewhat different body proportions, colour patterns, and diets (Shine, 1987c; Cogger, 1992), but they are unique among the viviparous Australian elapids in the possession of a divided anal plate and single subcaudal scales (Shine, 1985). Based on morphological (McDowell, 1967; Wallach, 1985), karyological, and electrophoretic (Mengden, 1985a), and mitochondrial DNA sequence data (Keogh *et al.*, 1998), *Hemiaspis* monophyly is strongly supported. Hemipenial morphology corroborates their close relationship, but it is interesting to note that hemipenial morphology unites not only *Hemiaspis* species, but also these two species with *Drysdalia.* All six species display a simple cylindrical hemipenis with only weakly differentiated apical lobes and a distinct spine line. However, a close relationship between these genera has not previously been suggested or implied by other phylogenetic studies. Further, while *Hemiaspis* monophyly has been well supported, *Drysdalia* monophyly has been questioned by diverse data sets, despite the four species appearing to form a fairly well defined group (Coventry & Rawlinson, 1980). Based on morphological data, McDowell (1967) suggested that *D. coronata* shares a closer relationship with *Notechis* than its congeners, going so far as to suggest that generic level distinction might be warranted. The distinctiveness of *D. coronata* was corroborated by karyotype data with the other three *Drysdalia* species sharing a karyomorph group with *Denisonia* (Mengden, 1985a). *Drysdalia coronata* differs from its congeners in diet as well, taking both anurans and scincid lizards in approximately equal proportions while other *Drysdalia* feed primarily on scincid lizards (Shine, 1981b). However, electrophoretic data united all *Drysdalia* species except *D. coronata* with the *Notechis* lineage (Mengden, 1985a, fig. 3), and mitochondrial DNA sequence data suggest that *D. coronoides* shares a close relationship with the *Notechis* lineage while *D. coronata* is more closely related to *Hemiaspis, Rhinoplocephalus* and *Suta* (Keogh *et al.*, 1998). Despite the shared hemipenial type of the four *Drysdalia* species, the weight of the evidence seems to suggest that *Drysdalia* is paraphyletic, and the nature of *Drysdalia* affinities remains unclear. However, it is worth nothing that the hemipenes of all *Drysdalia* and *Hemiaspis* species are clearly distinct from *Notechis* as well as from *Denisonia.*

Rhinoplocephalus and *Suta*

The species currently assigned to *Rhinoplocephalus* and *Suta* have had a complicated, unstable, and highly interlinked taxonomic history. The species currently assigned to *Rhinoplocephalus* and *Suta* (as defined by Hutchinson, 1990) have been placed in no fewer than five other genera including *Cryptophis*, *Denisonia*, *Hoplocephalus*, *Parasuta*, and *Unechis* (see the comprehensive taxonomic review by Mengden [1983] and also Cogger *et al.* [1983] and Hutchinson [1990] for further taxonomic comments on this group). Given the number of taxonomic re-arrangements and the data on which they were based, it is clear that the lines of demarcation between various groups are weak and the taxonomic conclusions have been highly subjective. Storr (1981) noted that there were as many taxonomic opinions as there have been researchers on this group—and then he presented a new arrangement. The taxonomic shuffling is due largely to differing emphasis being put on the relatively few taxonomic characters used by various authors (Mengden, 1983). Though there has been considerable disagreement on the nature of interspecific relationships, more recent studies have partially remedied this problem and there is now general consensus that the members of *Rhinoplocephalus* and *Suta* are each other's closest relatives (Wallach, 1985; Mengden, 1985a, Hutchinson, 1990; Keogh *et al.*, 1998). Whatever the relationships between these species, hemipenial morphology unambiguously supports monophyly of a *Rhinoplocephalus–Suta* clade with the hemipenes of all members essentially identical. The *Rhinoplocephalus–Suta* clade is united by the unique presence of a large fleshy medial projection between the apical lobes. It is worth noting that in addition to their morphological similarity, *Rhinoplocephalus* and *Suta* also are ecologically cohesive, inhabiting similar habitat types and feeding primarily on small lizards (Shine, 1984b, 1986, 1988). Given the highly conservative nature of hemipenial variation within the group, various subgroups within this clade proposed by other authors are neither supported nor refuted by hemipenial morphology. However, it is important to note that *S. fasciata* and *S. punctata*, species sometimes associated with *Denisonia*, are clearly part of the *Suta–Rhinoplocephalus* clade. This is in agreement with McDowell (1967), Wallach (1985), Mengden (1985a), Shine (1985) and Schwaner *et al.* (1985), each of whom found reason to associate these two species with taxa now placed in *Suta* and *Rhinoplocephalus*.

Though groups six (*Drysdalia* and *Hemiaspis*) and seven (*Rhinoplocephalus* and *Suta*) each display unique aspects of hemipenial morphology, the four genera share a very similar organ with the only significant difference between the groups being the presence of a medial projection protruding from between the apical lobes in *Rhinoplocephalus* and *Suta*.

Acanthophis and *Denisonia*

Acanthophis is arguably the most highly derived clade within the terrestrial Australian elapid lineage. The three currently recognized species are united by a number of non-hemipenial synapomorphies, character states that not only distinguish them from other elapids but also are remarkably convergent upon the Viperidae (Shine, 1980b). Hemipenial morphology also is unique in *Acanthophis*. Three features in particular are notable. First, the hemipenes of *Acanthophis* are the only ones I have classified as 'deeply forked' (Fig. 7A). Second, each apical lobe is almost perfectly cylindrical. Even more striking are the smooth, flat, disk-shaped distal portions of the apical lobes. This feature, unique to *Acanthophis* among the terrestrial Australian

elapids, was noted long ago. Cope (1893) stated the organ ". . . is reticulate at the extremities and spinous below, in *Calliophis* [*Maticora*] *bivirgatus*, *Naja*, *Acanthophis*, *Bungarus*, and *Sepedon* [*Hemachatus*], the apex smooth in the two genera last named". However, it appears that Cope may have inadvertently reversed the order of at least *Acanthophis* and *Bungarus* in his list as *Bungarus* does not display the smooth apical lobes (Slowinski, 1994) seen in *Acanthophis*. I have not studied *Hemachatus* hemipenes. The hemipenis of *Acanthophis* also has been briefly described by Covacevich *et al.* (1981), who compared it to *Oxyuranus* when demonstrating hemipenial differences between the groups. In *Acanthophis* they noted the lack of a major spine line, the bifurcation of the sulcus spermaticus within the zone of small spines, the smooth basal portion and ". . . has the distal end of the organ conspicuously forked, with the tip of each lobe smooth." Like *Acanthophis*, *Denisonia maculata* and *D. devisi* are distinctive members of the terrestrial Australian elapid fauna. These small and thick-set snakes are morphologically (Wallach, 1985) and chromosomally distinctive (Mengden, 1985a, b) and ecologically similar (Shine, 1983). In addition, they share a hemipenial morphology unique among the terrestrial Australian elapids. Though not as extreme as *Acanthophis*, *Denisonia* possess a deeply bifurcated hemipenis. The rounded and bulbous apical lobes and flat top are very similar to that of *Acanthophis* (Fig. 7B).

Acanthophis and *Denisonia* each have unique hemipenial synapomorphies; however, of the various hemipenial types here described, those of *Acanthophis* and *Denisonia* are much more similar to each other than to any other terrestrial Australian elapid. Thus, I have placed them together in the same hemipenial group. These genera also share certain unique features among the terrestrial Australian elapids including short, thickset bodies with wide and large heads, elliptical pupils and similar foraging strategies (both are thought to be primarily sit-and-wait predators). However, it remains to be seen if these and hemipenial similarities are synapomorphies or simple convergences. The phylogenetic positions of both *Acanthophis* and *Denisonia* with respect to other terrestrial Australian elapids remain unclear. Due partly to the highly specialized morphology of *Acanthophis* and *Denisonia*, their relationship to other Australian elapids has been controversial. *Acanthophis* possess what Mengden (1985), b) interpreted as the probable ancestral karyotype ($2n = 36$ with 16 macrochromosomes and 20 microchromosomes) and he united *Acanthophis* with *Echiopsis* based presumably on the perceived importance of the $2 + 4$ temporal scale formula that *Acanthophis* and *Echiopsis* share, and the similar venom properties identified between the genera (Marshal & Herrman, 1984). Wallach (1985) placed *Acanthophis* as the sister group to my concept of the *Notechis* lineage, though noting the highly derived nature of the genus and postulating that perhaps *Acanthophis* had experienced higher rates of evolutionary change relative to the *Notechis* group. Moreover, *Acanthophis* is not particularly close immunologically to any other Australian elapid (Schwaner *et al.*, 1985). Similarly, the placement of *Denisonia* relative to other Australian elapids is unclear with other data sets uniting the genus with *Drysdalia* (Wallach, 1985; Mengden, 1985a – karyotype data) or *Echiopsis* (Mengden, 1985a – electrophoretic data – his figure 3). Wallach (1985) implied the highly tenuous nature of his hypothesis of *Denisonia* relationships. Unfortunately, mitochondrial DNA sequence data further cloud the issue with *Acanthophis* and *Denisonia* variously united as a clade or being closely associated with *Echiopsis* as well as *Rhinoplocephalus*, *Suta*, and *Drysdalia coronata* (Keogh *et al.*, 1998). Despite these results, given the very strong similarity between *Acanthophis* and *Denisonia* in hemipenes, as well as in other

morphological and ecological attributes, and the association of these genera in analyses of mitochondrial DNA sequences (Keogh *et al.*, 1998), the weight of evidence would seem to tip the balance toward a closer affinity between these genera than with other taxa.

Higher level relationships

Based primarily on ecological data, Shine (1985) pointed out that a large portion of the terrestrial Australian elapids might be comprised of a single (monophyletic) lineage defined by viviparity and single as opposed to divided anal scales, to the exclusion of the oviparous species. This hypothesis was largely supported by the studies of Mengden (1985a), Schwaner *et al.* (1985) and Wallach (1985) (see Fig. 9). My hemipenial groups one through four are each comprised of oviparous species (except *Pseudechis porphyriacus* which represents a separate evolution of viviparity: Mengden *et al.*, 1986; Shine, 1987d), and groups five through eight are each comprised of viviparous species. The viviparous taxa might indeed constitute a clade, and it is important to note that the hemipenial groups are comprised of *either* oviparous or viviparous taxa. However, hemipenial data neither clearly support nor refute this higher-level division among the Australian elapids as it does provide any synapomorphy which unites all the viviparous species.

ACKNOWLEDGEMENTS

This study would not have been possible without the help and cooperation of the curators and collection managers associated with each of the major Australian museums. For their time and encouragement I thank Mark Hutchinson and Adrienne Edwards (South Australian Museum), Allen Greer and Ross Sadlier (Australian Museum), Ken Aplin and Laurie Smith (Western Australian Museum), Paul Horner (Northern Territory Museum of Arts and Sciences), Jeanette Covacevich and Paul Couper (Queensland Museum), John Wombey (CSIRO), and John Coventry (National Museum of Victoria). For numerous stimulating discussions I thank Rick Shine, Paul Doughty, Hamlet Giragossyan, Peter Harlow, Steve Donnellan, Mark Hutchinson, Tony Frankino, Glen Shea, Joanne Keogh, and the curators and collections managers mentioned above. The manuscript was improved by the constructive criticism of Chris Austin, Bill Branch, Steve Cooper, Steve Donnellan, Ralph Foster, Mark Hutchinson, Michael Mahony, Al Savitzky, Rick Shine, Van Wallach and an anonymous reviewer. This study would have been much less comprehensive if not for the efforts of Terry Schwaner in helping assemble the South Australian Museum's hemipenis collection. My research was supported by an Australian Museum Postgraduate Research Grant, The Ethel Mary Read Fund of the Royal Zoological Society of New South Wales, the James Kentely Memorial Fund, and the Society for the Study of Amphibians and Reptiles. It was conducted while I was supported by a Fulbright Fellowship from the American-Australian Education Foundation, an Overseas Postgraduate Research Scholarship, and a University of Sydney Postgraduate Research Award.

REFERENCES

Arnold EN. 1973. Relationships of the Palaearctic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammodromus* (Reptilia: Lacertidae). *Bulletin of the British Museum (Natural History) Zoology* **25:** 289–366.

Arnold EN. 1983. Osteology, genitalia and the relationships of *Acanthodactylus* (Reptilia: Lacertidae). *Bulletin of the British Museum (Natural History), Zoology* **44:** 291–339.

Arnold EN. 1986a. The hemipenis of lacertid lizards (Reptilia: Lacertidae): Structure, variation and systematic implications. *Journal of Natural History* **20:** 1221–1257.

Arnold EN. 1986b. Why copulatory organs provide so many useful taxonomic characters: The origin and maintenance of hemipenial differences in lacertid lizards (Reptilia: Lacertidae). *Biological Journal of the Linnean Society* **29:** 263–281.

Bailey JR. 1967. The synthetic approach to colubrid classification. *Herpetologica* **23:** 155–161.

Bellairs AdA., Underwood G. 1951. The origin of snakes. *Biological Review* **26:** 193–237.

Bogert CM. 1940. Herpetological results of the Vernay Angola Expedition, with notes on African reptiles in other collections. Part 1. Snakes, including an arrangement of African Colubridae. *Bulletin of the American Museum of Natural History* **77:** 1–107.

Böhme W. 1971. Uber das Stachelepithel am Hemipenis lacertider Eidechsen und seine systematische Bedeutung. *Zeitschrift fur zoologische Systematik und Evolutionsforschung* **9:** 187–223.

Böhme W. 1988. Zur genitalmorphologie der sauria: Funktionelle und stammesgeschichtliche aspekte. *Bonner Zoologische Monographien*, No. **27:** 1–176.

Boulenger GA. 1896. *Catalogue of Snakes of the British Museum (Natural History)*. Volume 3. London: British Museum of Natural History.

Branch WR, Wade EOZ. 1976. Hemipenial morphology of British snakes. *British Journal of Herpetology* **5:** 548–553.

Branch WR. 1981. Hemipenes of the Madagascan Boas *Acrantophis* and *Sanzinia*, with a review of hemipeneal morphology in the Boinae. *Journal of Herpetology* **15:** 91–99.

Branch WR. 1982. Hemipeneal morphology of Platynotan lizards. *Journal of Herpetology* **16:** 16–38.

Branch WR. 1986. Hemipenial morphology of African snakes: a taxonomic review Part 1. Scolecophidia and Boidae. *Journal of Herpetology* **20:** 285–299.

Cadle JE. 1982. Problems and approaches in the interpretation of the evolutionary history of venomous snakes. *Memorias del Instituto Butantan* **46:** 255–274.

Cadle JE. 1988. Phylogenetic relationships among advanced snakes. *University of California Publications in Zoology* **119:** 1–77.

Cadle JE. 1994. The colubrid radiation in Africa (Serpentes: Colubridae): Phylogenetic relationships and evolutionary patterns based on immunological data. *Zoological Journal of the Linnean Society* **110:** 103–140.

Cadle JE. 1996. Snakes of the genus *Liopholidophis* (Colubridae) from Eastern Madagascar: New species, revisionary notes, and an estimate of phylogeny. *Bulletin of the Museum of Comparative Zoology* **154:** 369–464.

Cadle JE, Sarich V. 1981. An immunological assessment of the phylogenetic position of New World coral snakes. *Journal of Zoology, London* **195:** 157–167.

Cadle JE, Gorman GC. 1981. Albumin immunological evidence and the relationships of sea snakes. *Journal of Herpetology* **15:** 329–334.

Card W, Kluge AG. 1995. Hemipeneal skeleton and varanid lizard systematics. *Journal of Herpetology* **29:** 275–280.

Clark Jr. DR. 1964. The structures of the hemipenis as systematic characters in the genus *Virginia* Baird and Girard. *Herpetologica* **20:** 33–37.

Cogger HG. 1985. Australian proteroglyphous snakes—An historical overview. In: Grigg G, Shine R and Ehmann H, eds. *Biology of Australian Frogs and Reptiles*. Sydney: Surrey Beatty and Sons, 143–154.

Cogger HG. 1992. *Reptiles and Amphibians of Australia, 5th Edition*. Chatswood (Australia): Reed Books.

Cogger HG, Cameron EE, Cogger HM. 1983. *Amphibia and Reptilia, Vol. 1*. Canberra: Australian Government Publishing Service.

Cogger HG, Heatwole H. 1981. The Australian reptiles: Origins, biogeography, distribution patterns and island evolution. In: Keast A, ed. *Monographiae Biologicae Vol 41. Ecological Biogeography of Australia Vol 2*. The Hague: Junk, 1331–1374.

Cope ED. 1893. Prodromus of a new system of the non-venomous snakes. *American Naturalist* **28:** 477–483.

Cope ED. 1894. The classification of snakes. *American Naturalist* **28:** 831–844.

Cope ED. 1895. The classification of the Ophidia. *Transactions of the American Philosophical Society* **28:** 186–219.

Cope ED. 1896. On the hemipenis of the Sauria. *Proceedings of the Academy of Natural Sciences of Philadelphia* **1896:** 461–467.

Cope ED. 1900. The crocodilians, lizards and snakes of North America. Report of the United States National Museum, *Washington* **1898:** 153–1294.

Coulter AR, Harris RD, Sutherland SK. 1981. Enzyme immunoassay and radioimmunoassay: Their use in the study of Australian and exotic snake venoms. In: Banks CA, Martin AA, eds. *Proceedings of the Melbourne Herpetological Symposium*. Melbourne, 39–43.

Covacevich J, McDowell SB, Tanner C, Mengden GA. 1981. The relationship of the Taipan, *Oxyuranus scutellatus*, and the small-scaled snake, *Oxyuranus microlepidotus* (Serpentes: Elapidae). In: Banks CA, Martin AA, eds. *Proceedings of the Melbourne Herpetological Symposium*. Melbourne, 160–168.

Coventry AJ, Rawlinson PA. 1980. Taxonomic revision of the elapid snake genus *Drysdalia* Worrell 1961. *Memoirs of the National Museum Victoria* **41:** 65–78.

Domergue CA. 1962. Observations sur les pénis de ophidiens (Deuxième note). *Bulletin de la Société des Sciences Naturelles et Physiques du Maroc* **42:** 87–106.

Dowling HG. 1959. Apical papillae on the hemipenis of two colubrid snakes. *American Museum Novitates* No. **1948:** 1–7.

Dowling HG. 1967. Hemipenes and other characters in colubrid classifications. *Herpetologica* **23:** 138–142.

Dowling HG. 1974. A provisional classification of snakes. In: Dowling HG, ed. *1974 Yearbook of Herpetology* New York: HISS Publications, 167–170.

Dowling HG, Duellman WE. 1978. *Systematic Herpetology: A Synopsis of Families and Higher Categories*. New York: HISS Publications.

Dowling HG, Savage JM. 1960. A guide to the snake hemipenis: A survey of basic structure and systematic characters. *Zoologica* **45:** 17–28.

Dunn ER. 1928. A tentative key and arrangement of the American genera of Colubridae. *Bulletin of the Antivenin Institute of America* **2:** 18–24.

Eberhard WG. 1985. *Sexual selection and animal genitalia*. Cambridge MA: Harvard University Press.

Fohlman J. 1979. Comparison of two highly toxic Australian snake venoms: The taipan (*Oxyuranus s. scutellatus*) and the fierce snake (*Parademansia microlepidotus*). *Toxicon* **17:** 170–172.

Gillam MW. 1979. The genus *Pseudonaja* (Serpentes: Elapidae) in the Northern Territory. *Territory Parks and Wildlife Research Bulletin* **1:** 1–28.

Golay P, Smith HM, Broadley DG, Dixon JR, McCarthy C, Rage JC, Schatti B, Toriba M. 1993. *Endoglyphs and other major venomous snakes of the world. A checklist*. Azemiops: S.A. Switzerland.

Günther A. 1858. *Catalogue of the Colubrine Snakes in the Collection of the British Museum*. London: British Museum.

Hutchinson MN. 1990. The generic classification of the Australian terrestrial elapid snakes. *Memoirs of the Queensland Museum* **28:** 397–405.

Jenner JV, Dowling HG. 1985. Taxonomy of American Xenodontine snakes: The tribe Pseudoboini. *Herpetologica* **41:** 161–172.

Keogh JS. 1996. Origin of the hemipenis *retractor penis magnus* muscle: Evidence for utility in snake systematics. *The Snake* **27:** 114–119.

Keogh JS, Smith SA. 1996. Taxonomy and natural history of the Australian bandy-bandy snakes (Elapidae: *Vermicella*) with the description of two new species. *Journal of Zoology, London* **240:** 677–701.

Keogh JS. 1997. Phylogenetic studies on Australo-Papuan elapid snakes based on morphology and DNA. Unpublished Ph.D dissertation. University of Sydney, Australia.

Keogh JS. 1998. Molecular phylogeny of elapid snakes and a consideration of their biogeographical history. *Biological Journal of the Linnean Society* **63:** 177–203.

Keogh JS, Shine R, Donnellan S. 1998. Phylogenetic relationships of terrestrial Australo-Papuan elapid snakes based on cytochrome *b* and 16S rRNA sequences. *Molecular Phylogenetics and Evolution* **10:** 67–81.

Kinghorn JR. 1956. *The Snakes of Australia*. Second Edition. Sydney: Angus and Robertson.

Klaver C, Böhme W. 1986. Phylogeny and classification of the Chamaeleonidae (Sauria) with special reference to hemipenis morphology. *Bonner Zoologische Monographien* No. **22:** 1–64.

Knight A, Mindell DP. 1994. On the phylogenetic relationships of Colubrinae, Elapidae, and Viperidae and the evolution of front-fanged venom systems in snakes. *Copeia* **1994:** 1–9.
Krefft G. 1869. *Snakes of Australia.* Sydney: Government Printer.
Loveridge A. 1934. Australian reptiles in the Museum of Comparative Zoology. *Bulletin of the Museum of Comparative Zoology* **77:** 241–383.
Mackay RD. 1955. A revision of the genus *Pseudechis*. *Proceedings of the Royal Zoological Society of New South Wales*. **1953–1954:** 15–23.
Mao SH, Chen BY, Chang HM. 1977. The evolutionary relationships of sea snakes suggested by immunological cross-reactivity of transferrin. *Comparative Biochemistry and Physiology* **57A:** 403–406.
Mao SH, Dessauer HC, Chen BY. 1978. Fingerprint correspondence of hemoglobins and the relationships of sea snakes. *Comparative Biochemistry and Physiology* **59B:** 353–361.
Mao SH, Chen BY, Yin FY, Guo YW. 1983. Immunotaxonomic relationships of sea snakes and terrestrial elapids. *Comparative Biochemistry and Physiology* **74A:** 869–872.
Mao SH, Yin FY, Guo YW. 1984. The hemipenis of common Taiwanese venomous snakes. *Herpetologica* **40:** 406–410.
Marshal LR, Hermann RP. 1984. Envenomation by the Bardick (*Echiopsis curtis*) snake and cross-reactivity with death adder antivenom using the snake detection kit. *Medical Journal of Australia* **140:** 541–542.
McCann C. 1946. The hemipenis of reptiles. *Journal of the Bombay Natural History Society* **46:** 348–373.
McCarthy CJ. 1985. Monophyly of the elapid snakes (Serpentes: Reptilia). An assessment of the evidence. *Zoological Journal of the Linnean Society* **83:** 79–93.
McDowell SB. 1961. (Review of) Systematic division and evolution of the colubrid snake genus Natrix, with comments on the subfamily Natricinae, by Edmond V. Malnate. *Copeia* **1961:** 502–506.
McDowell SB. 1967. *Aspidomorphus*, a genus of New Guinea snakes of the family Elapidae, with notes on related genera. *Journal of Zoology, London* **151:** 497–543.
McDowell SB. 1968. Affinities of the snakes usually called *Elaps lacteus* and *E. dorsalis*. *Zoological Journal of the Linnean Society* **47:** 561–578.
McDowell SB. 1969a. *Toxicocalamus*, a New Guinea genus of snakes of the family Elapidae. *Journal of Zoology, London* **159:** 443–511.
McDowell SB. 1969b. Notes on the Australian sea-snake *Ephalophis greyi* M. Smith (Serpentes: Elapidae, Hydrophiinae) and origin and classification of sea-snakes. *Zoological Journal of the Linnean Society* **48:** 333–349.
McDowell SB. 1970. On the status and relationships of the Solomon Island elapid snakes. *Journal of Zoology, London* **151:** 145–190.
McDowell SB. 1972. The genera of sea-snakes of the *Hydrophis* group (Serpentes: Elapidae). *Transactions of the Zoological Society of London* **32:** 189–247.
McDowell SB. 1986. The architecture of the corner of the mouth of colubroid snakes. *Journal of Herpetology* **20:** 353–407.
McDowell SB. 1987. Systematics. In: Siege RA, Collins JT, Novak SS, eds. *Snakes: Ecology and Evolutionary Biology* New York: McGraw Hill, 3–50.
Mengden GA. 1982. Chromosomal evolution and the phylogeny of elapid snakes. Ph.D. Dissertation, Australian National University, Canberra.
Mengden GA. 1983. The taxonomy of Australian elapid snakes, a review. *Records of the Australian Museum* **35:** 195–222.
Mengden GA. 1985a. Australian elapid phylogeny: A summary of the chromosomal and electrophoretic data. In: Grigg G, Shine R, Ehmann H, eds. *Biology of Australasian Frogs and Reptiles*. Sydney: Surrey Beatty and Sons, 185–192.
Mengden GA. 1985b. A chromosomal and electrophoretic analysis of the genus *Pseudonaja*. In: Grigg G, Shine R, Ehmann H, eds. *Biology of Australasian Frogs and Reptiles*. Sydney: Surrey Beatty and Sons, 193–208.
Mengden GA, Shine R, Moritz C. 1986. Phylogenetic relationships within the Australasian venomous snakes of the genus *Pseudechis*. *Herpetologica* **42:** 215–229.
Minton SA. 1981. Evolution and distribution of venomous snakes. In: Banks CA, Martin AA, eds. *Proceedings of the Melbourne Herpetological Symposium. Melbourne* 55–59.
Minton SA, da Costa MS. 1975. Serological relationships of sea snakes and their evolutionary implications. In: Dunson W, ed. *The Biology of Sea Snakes*. Baltimore: University Park Press, 33–55.
Myers CW, Trueb L. 1967. The hemipenis of an anomalepidid snake. *Herpetologica* **23:** 235–238.
Myers CW, Campbell JA. 1981. A new genus and species of colubrid snake from the Sierra Madre del Sur of Guerrero, Mexico. *American Museum Novitates* **2708:** 1–20.

Presch W. 1978. Descriptions of the hemipenial morphology in eight species of microteiid lizards (family Teiidae, subfamily Gymnophthalminae). *Herpetologica* **34:** 108–112.

Rasmussen AR. 1994. A cladistic analysis of *Hydrophis* subgenus *Chitulia* (McDowell, 1972) (Serpentes, Hydrophiidae). *Zoological Journal of the Linnean Society* **111:** 161–178.

Rawlinson PA. 1991. Taxonomy and distribution of the Australian tiger snakes (*Notechis*) and copperheads (*Austrelaps*) (Serpentes: Elapidae). *Proceedings of the Royal Society of Victoria* **103:** 125–135.

Robb J. 1960. The internal anatomy of *Typhlops* Schneider (Reptilia). *Australian Journal of Zoology* **8:** 181–216.

Robb J. 1966a. The structure and possible function of the cloacal pouches of male Australian typhlopids. *Australian Journal of Zoology* **14:** 27–30.

Robb J. 1966b. The generic status of the Australasian typhlopids (Reptilia: Squamata). *Annals and Magazine of Natural History, Series 13*. **9:** 675–679.

Rosenberg HI. 1967. Hemipenial morphology of some amphisbaenids (Amphisbaenia: Reptilia). *Copeia* **1967:** 349–361.

Savitzky AH. 1979. The origin of New World proteroglyphous snakes and its bearing on the study of venom delivery systems in snakes. Ph.D. Dissertation, University of Kansas: Lawrence.

Scanlon JD. 1985. Phylogeny and relationships of the elapid snake genus *Simoselaps* Jan, 1859: The evolution of a group of burrowing snakes. B.Sc (Honours), University of Sydney.

Scanlon JD, Shine R. 1988. Dentition and diet: Adaptations to oophagy in the Australian elapid genus *Simoselaps*. *Journal of Zoology* **216:** 519–528.

Schwaner TD, Baverstock PR, Dessauer HC, Mengden GA. 1985. Immunological evidence for the phylogenetic relationships of Australian elapid snakes. In: Grigg G, Shine R, Ehmann H, eds. *Biology of Australasian Frogs and Reptiles*. Sydney: Surrey Beatty and Sons, 177–184.

Shea GM, Shine R, Covacevich JC. 1993. Family Elapidae. In: Glasby CJ, Ross GJB, Beesley PL, eds. *Fauna of Australia*. Canberra: Australian Government Publishing Services, 295–309.

Shine R. 1980a. Comparative ecology of three Australian snake species of the genus *Cacophis* (Serpentes: Elapidae). *Copeia* **1980:** 831–838.

Shine R. 1980b. Ecology of the Australian death adder *Acanthophis antarcticus* (Elapidae): Evidence for convergence with the Viperidae. *Herpetologica* **36:** 281–289.

Shine R. 1981a. Ecology of Australian elapid snakes of the genera *Furina* and *Glyphodon*. *Journal of Herpetology* **15:** 219–224.

Shine R. 1981b. Venomous snakes in cold climates: Ecology of the Australian genus *Drysdalia* (Serpentes: Elapidae). *Copeia* **1981:** 14–25.

Shine R. 1983. Food habits and reproductive biology of Australian elapid snakes of the genus *Denisonia*. *Journal of Herpetology* **17:** 171–175.

Shine R. 1984a. Ecology of small fossorial Australian snakes of the genera *Neelaps* and *Simoselaps* (Serpentes, Elapidae). In: Seigel RA, Hunt LE, Knight JL, Maleret L and Zuschlag NL, eds. *Vertebrate Ecology and Systematics—A Tribute to Henry S. Fitch*. Lawrence: Museum of Natural History, University of Kansas, 173–183.

Shine R. 1984b. Reproductive biology and food habits of the Australian elapid snakes of the genus *Cryptophis*. *Journal of Herpetology* **18:** 33–39.

Shine R. 1985. Ecological evidence on the phylogeny of Australian elapid snakes. In: Grigg G, Shine R and Ehmann H, eds. *Biology of the Australasian Frogs and Reptiles* Sydney: Surrey Beatty and Sons, 255–260.

Shine R. 1986. Natural history of two monotypic snake genera of Southwestern Australia, *Elapognathus* and *Rhinoplocephalus* (Elapidae). *Journal of Herpetology* **20:** 436–439.

Shine R. 1987a. Ecological ramifications of prey size: Food habits and reproductive biology of Australian copperhead snakes (*Austrelaps*, Elapidae). *Journal of Herpetology* **21:** 21–28.

Shine R. 1987b. Ecological comparisons of island and mainland populations of Australian tigersnakes (*Notechis:* Elapidae). *Herpetologica* **43:** 233–240.

Shine R. 1987c. Food habits and reproductive biology of Australian snakes of the genus *Hemiaspis* (Elapidae). *Journal of Herpetology* **21:** 71–74.

Shine R. 1987d. The evolution of viviparity: Ecological correlates of reproductive mode within a genus of Australian snakes (*Pseudechis*: Elapidae). *Copeia* **1987:** 551–563.

Shine R. 1988. Food habits and reproductive biology of small Australian snakes of the genera *Unechis* and *Suta* (Elapidae). *Journal of Herpetology* **22:** 307–315.

Shine R, Charles N. 1982. Ecology of the Australian elapid snake *Tropidechis carinatus*. *Journal of Herpetology* **16:** 383–387.

Shine R, Covacevich J. 1983. Ecology of highly venomous snakes: The Australian genus *Oxyuranus* (Elapidae). *Journal of Herpetology* **17:** 60–69.
Slowinski JB. 1994. A phylogenetic analysis of *Bungarus* (Elapidae) based on morphological characters. *Journal of Herpetology* **28:** 440–446.
Slowinski JB. 1995. A phylogenetic analysis of the New World coral snakes (Elapidae: *Leptomicrurus*, *Micruroides* and *Micrurus*) based on allozyme and morphological characters. *Journal of Herpetology* **29:** 325–338.
Slowinski JB, Knight A, Rooney AP. 1997. A phylogenetic analysis of the Elapidae (Serpentes) based on phospholipase amino acid sequences. *Molecular Phylogenetics and Evolution* **8:** 349–362.
Smith HM, Smith RB, Sawin HL. 1977. A summary of snake classification (Reptilia: Serpentes). *Journal of Herpetology* **11:** 115–121.
Storr GM. 1967. The genus *Vermicella* (Serpentes: Elapidae) in Western Australia and the Northern Territory. *Journal and Proceedings of the Royal Society of Western Australia* **50:** 80–92.
Storr GM. 1979. Revisionary notes on the genus *Vermicella* (Serpentes: Elapidae). *Records of the Western Australian Museum* **8:** 75–79.
Storr GM. 1981. The *Denisonia gouldii* species-group (Serpentes: Elapidae) in Western Australia. *Records of the Western Australian Museum* **8:** 501–515.
Storr GM. 1982. The genus *Notechis* (Serpentes, Elapidae) in Western Australia. *Records of the Western Australian Museum* **9:** 325–340.
Storr GM. 1984. Revision of *Denisonia suta* (Serpentes: Elapidae) and the description of a new species closely related to it. *Records of the Western Australian Museum* **11:** 249–257.
Tamiya N. 1985. A comparison of amino acid sequences of neurotoxins and of phospholipases of some Australian elapid snakes with those of other proteroglyphous snakes. In: Grigg G, Shine R and Ehmann H, eds. *Biology of Australasian Frogs and Reptiles*. Sydney: Surrey Beatty and Sons, 209–219.
Underwood G. 1967a. *A Contribution to the Classification of Snakes*. London: Trustees of the British Museum (Natural History).
Underwood G. 1967b. A comprehensive approach to the classification of higher snakes. *Herpetologica* **23:** 161–168.
Underwood G, Kochva E. 1993. On the affinities of the burrowing asps *Atractaspis* (Serpentes: Atractaspididae). *Zoological Journal of the Linnean Society* **107:** 3–64.
Vellard JA. 1928a. Importance des caractères fournis par l'hemipenis pour la classification des Ophidiens. *Bulletin de la Société Zoologique de France* **53:** 406–418.
Vellard JA. 1928b. O Hemipenis dos ophidios. Importancia de sens caracteres para classificacao das serpentes. *Boletim do Instituto Vital Brazil* **6:** 1–19.
Vellard JA. 1946. Morfologia del hemipenis y evolucion de los ofidios. *Acta Zoologica Lilloana* **3:** 263–288.
Volsøe H. 1944. Structure and seasonal variation of the male reproductive organs of *Vipera berus* (L.). *Spolia Zoologica Musei Hauniensis* **5:** 1–157.
Voris HK. 1977. A phylogeny of the sea snakes (Hydrophiidae). *Fieldiana Zoology* **70:** 79–166.
Wallach V. 1985. A cladistic analysis of the terrestrial Australian elapidae. In: Grigg G, Shine R and Ehmann H, eds. *Biology of the Australasian Frogs and Reptiles*. Sydney: Surrey Beatty and Sons, 223–253.
Worrell E. 1955. A new elapine snake from Queensland. *Proceedings of the Royal Zoological Society of New South Wales* **1953–1954:** 41–43.
Worrell E. 1956. Notes on skull characters of some Australian snakes. *Australian Zoologist* **12:** 205–210.
Worrell E. 1960. A new species of *Denisonia*. *Proceedings of the Royal Zoological Society of New South Wales* **1958–1959:** 54–55.
Worrell E. 1961. Herpetological name changes. *Western Australian Naturalist* **8:** 18–27.
Worrell E. 1963a. A new elapine generic name. *Australian Reptile Park Records* **1:** 1–7.
Worrell E. 1963b. *Reptiles of Australia*. Sydney: Angus and Martin.
Worrell E. 1963c. Some new Australian reptiles (Part 1). Two new Australian subspecies of the elapine genus *Notechis* from Bass Strait. *Australian Reptile Park Records* **2:** 1–11.
Zaher H. 1994. Comments of the evolution of the jaw adductor musculature of snakes. *Zoological Journal of the Linnean Society* **111:** 339–384.

APPENDIX

Museum specimens examined in this study. Taxonomy follows Hutchinson (1990). Museum acronyms are as follows and are listed in this order: South Australian Museum (SAM), Australian Museum (AM), Northern Territory Museum of Arts and Sciences (NTM), Queensland Museum (QM), National Museum of Victoria (NMV), Western Australian Museum (WAM), CSIRO Australian National Wildlife Collection (ANWC). Not all museum specimens listed below displayed well everted hemipenes, some possessed only partially everted or badly prepared hemipenes. When this was the case, only unaffected characteristics were scored (such as base nudity, presence of spine line, etc).

Acanthophis antarcticus: SAM 19229, 24221, 28460, 30497, AM 95467, 98715, 111635, 125320, NTM 475, 8378, 9699, 9723, 9765, 31212, WAM 113130. *Acanthophis praelongus*: QM 54143. *Austrelaps* complex: SAM 19835, 19833, 20740, 21418, 21439, 21440, 22745, 23520, 23595, 23597, 23906, 23598, 23810, 25052, 25113, 25120, 25325, 25366, 26421, 27286, 28638, 30298, 30299, AM 3734, 47445, 54404, 54435, 54819, 58370, 61384, 70170, 80564, 89389, 89391, 93462, 107232, 107233, 107236, 107237, 107238, 111016, 121993, 142905, NMV 14700, 33102, 33409, 38750, 38754, 40057, 40076, 47639, 47647, 47649, 48773, 52131; ANWC 2812. *Cacophis squamulosus*: AM 47779, 76177, 81727, 115255, QM 26352. *Demansia atra*: SAM 29954, AM 55039, 56661, 97515, 105280, 107091, 110374, 121152, ANWC 5419, 5457, 5458, 5481. *Demansia olivacea*: AM 30094, NTM 6489, 7003, 8182, 16139. *Demansia papuensis*: AM 139881, NTM 144, 3124, 3528, 6882, 10683, QM 40262. *Demansia psammophis*: SAM 19587, 21430, 24930, 28451, AM 37048, 94781, 107549, 110365, 113994, NTM 1371, 3467, 5704, 5447. *Demansia psammophis reticulata*: SAM 18597, 28499, AM 140437. *Demansia torquata*: AM 111903, NTM 2077, 3642, QM 32744, 52516. *Denisonia devisi*: QM 5888, NMV 10560, 10562. *Denisonia maculata* (all dissected organs): AM 57272, 69973, 110474. *Drysdalia coronata*: SAM 22964, 22965, 22967, 22968, 22998, ANWC 2785. *Drysdalia coronoides*: SAM 22704, 29769, NMV 10935, 11776, 14300, 35771, 47527, ANWC 2821, 5046, 5105. *Drysdalia mastersi*: SAM 19939, 20611, 21956, 28079, NMV 25522, 52593, 53493, 54148, 54740, 59690, 59843. *Drysdalia rhodogaster*: ANWC 1225. *Echiopsis atriceps*: WAM 119225 (dissected organ). *Echiopsis curta*: SAM 22971, AM 42213, WAM 94802, 94803, 94804, 116278. *Elapognathus minor*: WAM 87905. *Furina diadema*: SAM 18160, 23268. *Furina dunmalli*: QM 34601, 34602, 47505. *Furina ornata*: SAM 26885, AM 117438, 119442, NMV 67492, WAM 63466. *Furina tristis*: AM 43914, QM 47574. *Hemiaspis dameli*: AM 11560, 65308, 110347, 110348, 125391. *Hemiaspis signata*: AM 96812, 12627, 29658, 37397, 47458, 67941, 95470, 76179, 103068, 110382, 139041, NMV 15311, ANWC 1279. *Hoplocephalus bungaroides*: ANWC 5040. *Hoplocephalus stephensi*: AM 58516. *Notechis complex*: SAM 1362, 18601, 18822, 18828, 18831, 19010, 19832, 19976, 21114, 21104, 21115, 21153, 21507, 22254, 22364, 22368, 22370, 22371, 22779, 22780, 22949, 23210, 23211, 23431, 23432, 23593, 23594, 23900, 23901, 23920, 23921, 24121, 24222, 24774, 24775, 24776, 24819, 25050, 25060, 25061, 25103, 25114, 25127, 25143, 25170, 25192, 25361, 26186, 26452, 26887, 26896, 27178, 27288, 27289, 27437, 27438, 30291, 30292, 30295, 30296, 30500, 30502, 30503, 30504, 30505, 30509, 30510, 30511, 30516, 30517, 30518, 30521, 31429, 31430, 31603, 31604, 31709, 31710, 31711, AM 19265, 61383, 71069, 73097, 96900, 103023, 104923, 106744, 111031, NTM 10954, WAM 89367 (located at SAM), 113306. *Oxyuranus microlepidotus*: SAM 20583, 26876, QM 50279, ANWC 5246. *Oxyuranus scutellatus*: SAM 24409, AM 56289, 56290, 80882, 105052, 142869, NTM 5125, ANWC 5246, 5372, 5467. *Pseudechis australis*: SAM 21190, 21192, 21193, 21194, 23282, 24118, 24123, 27013, 27014, 29577, 29908, 31703, AM 32628, 33300, 39974, 40555, 51944, 56831, 66568, 88943, 107230, 110515, 111021, 113131, 114272, 120846, 127890, 139849. *Pseudechis guttatus*: SAM 24416, AM 33227, 33228, 33292, 33295, 37368, 37369, 42159, 64775, 69976, 90345, 106808, 113961. *Pseudechis porphyriacus*: SAM 24127, 25056, 25294, 26189, 27131, and one SAM specimen with no registration number, AM 3837, 31798, 40356, 40357, 40552, 41800, 42157, 47514, 58926, 59928, 69091, 89259, 90352, 94913, 95370, 96199, 96899, 103818, 103820, 103828, 106809, 111026, 113958, 113962, 114593, 131976, 132780, 141447, 142837, 142838, 142873. *Pseudonaja affinis*: SAM 20605, 23002, 23003, 29476, 29484, 29509, 34340, AM 81342, 102050, 105535, 143064. *Pseudonaja guttata*: NTM 298, 466, 479, 582, 1455, 8607, QM 33141, 54264. *Pseudonaja inframaculata*: SAM 26145, 26474, 27057, 27058, 29026, 29530, 29531, 30386, 30387, 30399, 31574, 31597, 31599, 31600, 31693, 31694, 31695, 31696, 31698, 31700, 31702, AM 143068. *Pseudonaja ingrami*: AM 49236, NTM 464, 480, 596, 5203, 5220, QM 31905. *Pseudonaja modesta*: SAM 21026, 21028, 21191, 21954, 24656, 41769, 42962, AM 81386, 140450, NTM 521, 1854, WAM 120116. *Pseudonaja nuchalis*: SAM 18598, 18599, 18834, 18860, 18996, 20807, 20981, 21025, 21157, 21163, 21164, 21182, 21413, 21414, 22746, 24131, 24778, 24828, 25295, 28531, 28559, 29360, 29405, 29578, 31690, 31691, 31692, 31704, 34345, 34346, 36025, AM 10231, 49562, 50698, 51933, 51937,

51941, 51942, 64777, 80339, 90881, 90882, 96001, 97458, 98713, 101456, 101955, 105768, 117686, 117688, 119453, 127888, 131980, 140438, 140564, 146187. *Pseudonaja textilis*: SAM 18511, 18602, 18738, 18833, 19442, 19588, 19589, 19605, 19842, 19855, 20586, 20608, 20757, 20817, 21011, 21159, 21186, 21426, 21427, 21443, 21457, 23085, 23508, 23509, 23514, 24750, 24751, 24752, 24793, 24821, 24928, 24929, 24934, 24935, 24938, 24944, 25904, 26953, 28368, 28446, 28448, 29198, 30290, 31610, 31699, 31701, 31707, 32598, AM 3437, 6697, 29060, 31665, 31799, 33299, 37366, 39543, 47343, 47346, 47565, 49126, 49234, 59927, 51931, 59926, 60327, 65302, 67234, 69969, 69977, NTM 13, 312, 619, 5115, 5116, 6515, 12719, 17151. *Rhinoplocephalus bicolor*: AM 119473, 130623 WAM 34589, 42545. *Rhinoplocephalus boschmai*: AM 46030, 110371, 119423, 125405, ANWC 5042. *Rhinoplocephalus nigrescens*: SAM 23172, AM 92930, 92971, 93956, 93957, 95482, 95480, 95487, 95488, 95494, 95497, 103146, 103836, 105946, 105947, 110337, 119373, 119446, 119469, 119478, 130876, 138377. *Rhinoplocephalus nigrostriatus*: AM 63839, QM 22570. *Simoselaps anomalus*: WAM 116673, 70742. *Simoselaps approximans*: WAM 100592, 103387. *Simoselaps australis*: SAM 20759, 23086, AM 64696, 118878, 121989, NMV 57489, 60698, 60849, ANWC 5483. *Simoselaps bertholdi*: SAM 19830, 21431, 22603, 22604, 22605, 22972, 24764, 26205, 26214, 26215, 26181, AM 119376, 119459. *Simoselaps bimaculatus*: AM 119367, WAM 116665. *Simoselaps calonotus*: SAM 29765, AM 125365, WAM 87906. *Simoselaps fasciolatus*: SAM 18851, 20869, 21195, 26235, AM 82579, 130661, WAM 106152. *Simoselaps incinctus*: AM 130654, NTM 15572, 15574, 15586, 15588. *Simoselaps semifasciatus semifasciatus*: SAM 20789, 22825, 25917, 26883, 38756, NTM 3451, 5515 (as *S. s. roperi*), WAM 119198. *Suta fasciata*: WAM 83987, 113619, 116097. *Suta flagellum*: SAM 31626, 35990, AM 119413, 119414, 119415, NMV 15938, 15950, 15953, 15988, 15989. *Suta gouldi*: SAM 26109, 28367, 29767, 29768, AM 102724, 119391. *Suta monachus*: AM 105770, WAM 104427, 113365, 116594. *Suta nigriceps*: SAM 23919, 24086, 24141, 24924, 26107, 26113, 26114, 26116, 26886, 31565. *Suta ordensis*: NTM 561, WAM 58875, 76626. *Suta punctata*: SAM 29955, AM 46040, WAM 113576, 113622. *Suta spectabilis*: SAM 18159, 22409, 22484, 22485, 22487, 22488, 24148, 24142, 24144, 24147, 24085, 24571, 29515, 32493, 33353, AM 110478. *Suta spectabilis dwyeri*: AM 110338, 119425, 125390. *Suta suta*: SAM 19843, 21006, 23266, 24087, 25190, 26952, 27786, 28096, 28127, 28561, AM 37378, 37379, 46025, 51946, 64279, 76554, 92110, 110516, 119408, 119432, 125362, 129334, 138801, 140475, 141707, NTM 504, 577, 594, 1958, 2275, 4794, 9721, 17444, ANWC 948, 5048. *Tropidechis carinatus*: SAM 30596, QM 30435, 34118, ANWC 2818. *Vermicella annulata*: AM 37364, 49785, 82583, NMV 60761, 64983, ANWC 2810. *Vermicella intermedia*: SAM 27282, 29783, NTM 221.